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A CENSUS OF HOUSE MARTINS AND SWALLOWS NEAR MANCHESTER, 1933

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(*With three Figures in the Text.*)

INTRODUCTION.

DURING recent years, ornithologists from all parts of the country have reported a decrease in the numbers of nesting house martins (*Delichon urbica* (L.)) and swallows (*Hirundo rustica* L.). Many ancient nesting sites have been abandoned, and although new colonies have also been formed, it is doubtful whether they are equal in size and number to those deserted. Both species have a completely insectivorous diet, and are entirely beneficial, so that their decline has caused some concern, and numerous suggestions have been put forward to account for it. Some believe that the considerable slaughter of the migrating birds which occurs annually at numerous places on the Continent is largely responsible. Others suggest that modern civilisation is the real cause—the number of suitable nesting sites, particularly in the case of the swallow, being reduced by the continuous process of urbanisation, whilst the now almost universal method of tarring roads affects both the supply of mud for nesting purposes, and the insect life which is their sole source of food. A number of censuses taken over suitable areas and repeated at intervals would do much to prove the validity or otherwise of this latter explanation. Both species are conspicuous, and are particularly suitable for a nesting census of this type. The present census was taken in June and July, 1933, over an area of approximately 12¼ sq. miles to the south of Manchester.

DESCRIPTION OF THE AREA.

The area is irregular in shape, the boundaries being determined by the various main roads which are particularly convenient for census purposes. As shown by Fig. 1, much of the area is already closely built, and further extensive building operations are already in progress. Roughly speaking, the area works outward from the nineteenth-century suburb of Whalley Range, now an integral part of the city, to the former villages of Northenden, Gatley and Cheadle, which, although many houses are now being erected there, still retain considerable stretches of open country. At Wythenshawe a municipal housing estate is still in the process of erection, but an extensive park there has been preserved. Much of the open land along the River Mersey is given over to golf courses, playing fields, etc., and only on the southern boundary is there any extent of genuine arable and pasture land, the latter preponderating.

Although trees are fairly numerous in the southern portion, there are no extensive tracts of woodland.

The Mersey runs through the centre of the region, and there are a few small tributary streams. Insect life is always plentiful there, and hirundines and swifts are found feeding in large numbers. Owing to the low-lying nature of the land along its banks, only in a few cases are houses found close to the river. Except for this depression, the land is flat, about 100 ft. above sea-level.

Results of the census.

In the total area of 12¼ sq. miles 70 house martins' and 29–42 swallows' nests were discovered in June and July 1933. The figure for the swallows represents that 29 nests were actually seen; in the case of the other 13 definite evidence was obtained of their existence, but the actual nests were not located. This gives a density of 5·71 nests per sq. mile for the house martin, and 2·36–3·43 for the swallow. Although, as will be seen later, these total density figures are rather misleading, it is interesting to compare them with other census results. Alexander(**1**) in a census of house martins over 56 sq. miles near Oxford in 1931–2 found 27 pairs per sq. mile in the urban areas, whilst even the rural areas had from 9 to 10 pairs per square mile. Hollom(**3**) found 104 pairs of house martins and 52 pairs of swallows in 4 sq. miles largely pasture, at Bruton, Somerset, in 1929, a density of 26 and 13 pairs per sq. mile respectively. On repeating the count in 1931 there were 63 pairs of house martins and 60 of swallows, considerably reducing the density of house martins to 16 pairs per sq. mile and slightly increasing that of the swallows to 15 per sq. mile. Boyd(**2**) found 112 pairs of swallows in two rural townships in Cheshire, approximately 4¼ sq. miles in area, a density of 26 pairs per sq. mile.

The very low figures for the Manchester area are largely explained by an analysis of the exact distribution of the two species. This is well shown in the case of the house martin by Fig. 2. The distribution was very patchy—in large portions of the area they were entirely absent, while in a few districts they were abundant. Thus 36 nests, over 50 per cent. of the total, were concentrated in and around Gatley. In some cases, at least, the proximity of water appeared to be an important factor, since, as can be seen from Fig. 1, three colonies were located at the three points at which the belt of houses approaches nearest to the River Mersey, or its tributary brook. On the other hand, the concentration at Gatley does not appear to be due to this factor, and Northenden, a similar but rather bigger village, has a much smaller house martin population, in spite of the close proximity of the Mersey. Nor does it seem likely that the presence of the isolated colony at Baguley was due to the existence of the small and unimportant Baguley Brook. The complete absence of the bird from the Sale district is remarkable, but this may possibly be partially explained by the lack of water in that area. Alexander(**1**) suggests

that Oxford's abundant series of waterways may account for the fact that the population of house martins in Oxford is three times as dense as it is in the surrounding rural areas. Water usually means both food and nesting material, but the Gatley birds feed regularly close to and over the main road, and apparently find a satisfactory food supply there.

During the census, particular interest was taken in the age of the houses used for the house martins' nests in order to see whether they showed any

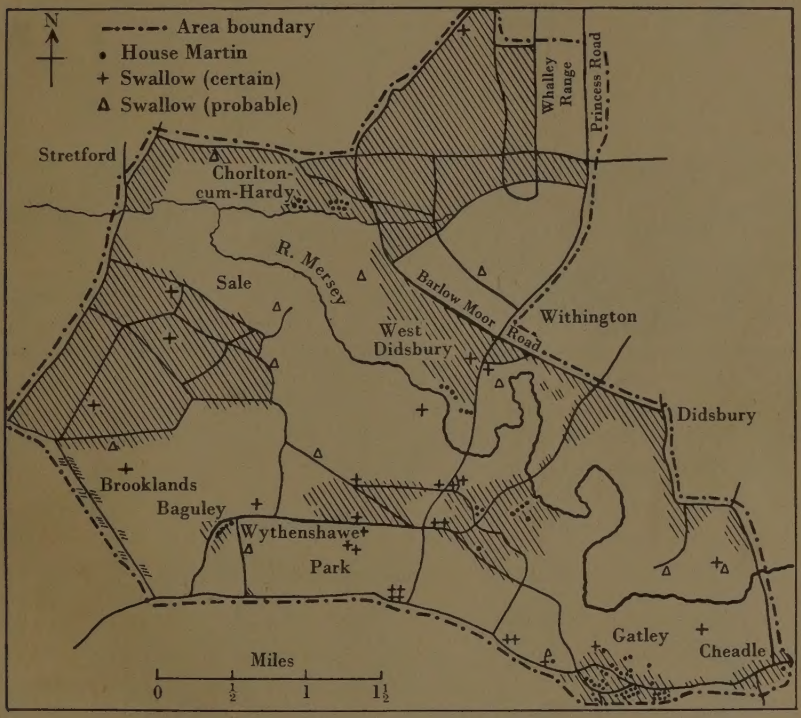

Fig. 1. Map of area, showing situation of nests.

readiness to colonise new sites. The majority of the nests were on houses at least 10 years old; the most recent being the 7 nests on the West Didsbury housing estate, which is about 4 years old. On the Wythenshawe estate many houses have been erected during the past year, but, although starlings, swifts and house sparrows have invaded the area, and nested in considerable numbers, no nests of the house martin were found. Although the majority of birds appeared to prefer houses with sharp-angled eaves, which afford a good support for a nest, on the West Didsbury estate right-angled eaves were

successfully used, they being the only type available in the immediate neighbourhood.

The average size of the house martin colonies was 2·18 nests, and their rather gregarious nature is shown by the following table:

Table I. *Size of house martin colonies.*

Colonies of	No. of colonies	Tota lNo. of nests
1 nest	15	15
2 nests	8	16
3 „	3	9
4 „	3	12
5 „	2	10
8 „	1	8
	32	70

The West Didsbury nests appear to be definite evidence of colonisation; before the housing estate was constructed, about 4 years ago, the only buildings were a farm-house and a golf-club-house, and the house martin does not usually nest in isolated dwellings.

Turning to the swallow, we found that it was far more widely distributed than the house martin (see Fig. 3), and that it did not seem to show the same dependence upon the presence of water. Although it was naturally commoner in the more open land, chiefly pasture for cattle, to the south, one nest was found in the extreme north of the area, within 2 miles of the centre of the city. Most of the nests were single, and little of the house martins' communal spirit was noticed, as the following figures show.

Table II. *Size of swallow colonies.*

Colonies of	No. of colonies	Total No. of nests
1 nest	34	34
2 nests	2	4
3 „	—	—
4 „	1	4
	37	42

Average size 1·13 nests.

The nests were harder to locate than those of the house martin, and the margin of error is therefore greater, though not, we think, above 20–30 per cent.

Within the area the two species did not appear to compete directly to any great extent, as can be seen from Figs. 2 and 3. Only 5 of the $\frac{1}{4}$ mile squares contain nests of both. Six contain those of house martin only, 18 the swallow only, and in 25 neither species nested. The swallow is often found near the farms, where cattle help to supply both food and mud. Nests were frequently found in cow-sheds and barns, but several were in house porches. Hollom (3)

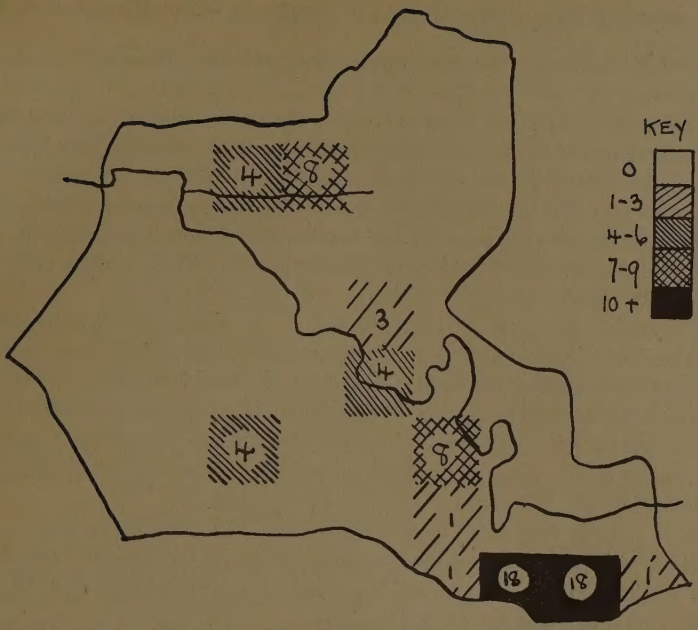

Fig. 2. Distribution of house martins. (1 square = $\frac{1}{4}$ sq. mile.)

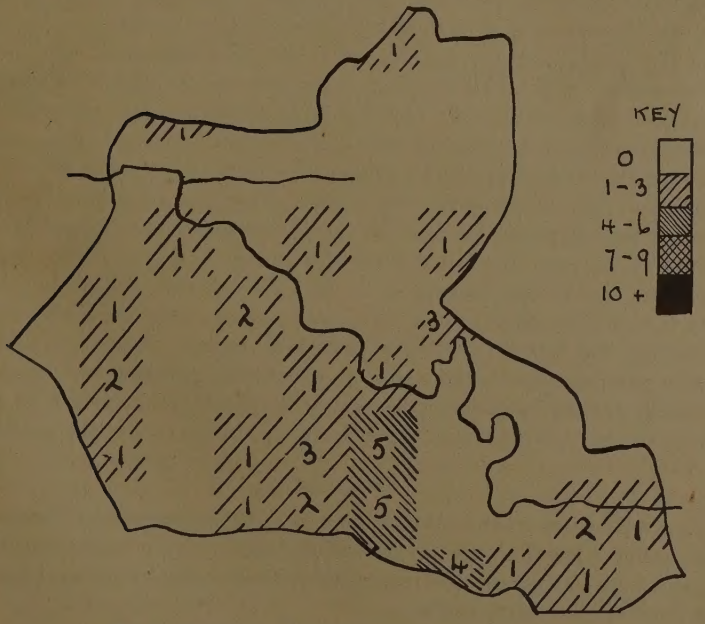

Fig. 3. Distribution of swallows. (1 square = $\frac{1}{4}$ sq. mile.)

found that the presence of cattle appeared to be favourable to swallows in Somerset.

The spread of houses appears to have a definite adverse effect upon the swallows. Until 1933 swallows were very common in Wythenshawe Park, and many pairs nested in the Hall and surrounding buildings. This year, with the completion of a large portion of the Wythenshawe housing estate nearby, they are noticeably scarcer, and only 3 nests were discovered within the whole park. Yet large areas of parkland, and presumably its attendant insect life, are still untouched.

The swift (*Apus apus* (L.)) appeared to be commoner than either the house martin or the swallow in most parts of the area, and with the exception of the solitary pair of swallows, penetrated furthest into the city—Whalley Range having at least two pairs. It appeared to have a very wide distribution, but unfortunately it proved impossible to make anything like a complete census of its nests. A definite increase of swifts was noted in the Wythenshawe neighbourhood in 1933 after the erection of the houses.

Sand martins only occur locally in the area. There are practically no sand or gravel pits in the district, and sandy portions of the banks of the Mersey form the most suitable sites. An imperfect count revealed at least 18 nests, all situated along the Mersey banks.

A single census is hardly sufficient to estimate accurately the effects of urbanisation on the house martin and swallow in the area. Nevertheless the one year's count may give us some indication of future tendencies. Alexander found that house martins were densest in the suburban areas, and perhaps the new colony at West Didsbury gives hope for the future of this species in the new suburban areas. Gilbert White(**4**) in a letter in 1773 remarked that house martins loved to frequent towns, especially if lakes and rivers were at hand, and that he had seen birds, dingy with soot, nesting even in Fleet Street and the Borough. Probably the embankment of the Thames and the increasing attention paid to sanitation affected their food supply, and helped to drive them away. In some London suburbs at least, the bird is more than holding its ground, and it may manage to do so in Manchester, though it is never likely to take as much advantage of man's presence as the house sparrow and the starling. The fate of the swallow seems more certain. Suburbs provide few suitable nesting sites, occasionally an odd stable perhaps, and cattle are necessarily absent. The striking decrease at Wythenshawe Park in 1933 would seem to suggest the usual result of urbanisation in the case of the swallow.

Summary.

1. A census was taken in 1933 in an area of 12¼ sq. miles near Manchester. Seventy house martins' and 29–42 swallows' nests were located: densities of 5·71 and 2·36–3·43 per sq. mile respectively. These densities are low compared with those of other areas studied.

2. The house martin, though the more abundant, was very local in its distribution, and the presence of water appeared in some cases to be a favourable factor.

3. The swallow was much more widespread, although commonest in the open country, chiefly pasture. Cattle appear to have a favourable influence on swallows.

4. The swallow frequents rural areas and the house martin urban districts.

5. It therefore seems likely that the increasing urbanisation of the area will cause a decrease in the number of swallows, but the house martin may to some extent hold its own.

We should like to express our thanks to Mr P. A. D. Hollom, who kindly supplied us with full details of his House Martin and Swallow Census at Bruton, Somerset, in 1929 and 1931, only a brief summary of which has been published.

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AN INVESTIGATION OF THE LITTORAL REGION OF WINDERMERE

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(From the Laboratory of the Freshwater Biological Association, Wray Castle, Windermere.)

(With Plate I and two Figures in the Text.)

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I. Introduction.

The following pages record an attempt to make a detailed survey of the fauna of a certain definite and sharply limited stretch of the lake shore. The object of the investigation was to discover the relation of the fauna to its environment, and at the same time to carry out some quantitative estimations of the numbers of animals present in certain areas.

The investigations were confined to what is usually called the "exposed littoral" portion of the lake shore. In this particular case the exposed littoral extends downwards to a depth of approximately 2 m. below the normal water-level of the lake. By "exposed littoral" is meant the zone of violent wave action. Below this zone is the "quiet littoral" which is usually taken as extending down to the limit of light penetration, below which rooted vegetation ceases to grow. In the following account the terms "shore" and "littoral" always refer to the exposed littoral unless otherwise stated.

The advantages of this classification are that it is applicable to any lake, and is based upon the most important factor in the littoral region, namely wave action.

II. Methods.

In the course of the investigation everything from sand to large boulders was encountered. Methods were devised so that the fauna in each type of habitat could be estimated quantitatively.

The standard area for this work was 1 sq. ft. In an environment of such varied character this is too small an area upon which to base counts. But a larger area would involve the moving of a quite impracticable amount of stone. The best way is to regard the figures of animal population given in the following pages as comparative results. It is reasonable, however, to suppose that the results do give an approximate conception of the numbers of actual population. It was only on sand or shingle that strictly quantitative results could be obtained.

For dealing with material varying from sand to boulders approximately 6 in. in diameter a small scoop was used. The scoop worked in such a manner that when it had been moved forward a certain distance, a known area of lake bed had been taken up. By means of a mechanical device the mouth of the scoop could be closed, thus preventing any material from being washed out. This scoop was found satisfactory up to a depth of $2\frac{1}{2}$ ft. It also had the additional advantage that the amount of material brought up could be varied according to circumstances. For dealing with large stones in $3\frac{1}{2}$–6 ft. of water, inaccessible with the small scoop, a large dredge devised by Mr Ullyott of the Freshwater Biological Laboratory was used. This also had a door which could be closed before the dredge was lifted. For taking samples at the lake edge a strong fire shovel was used, with a blade area of 14×14 in.

For dealing with the larger stones no mechanical contrivance was of any practical use. The stones were lifted by hand, and at the same time a large collecting net was slipped into the débris under the boulder. The use of this net is absolutely essential, because besides the clinging fauna of the stones, there is an unattached creeping fauna under the stones which would not be seen unless the net was used.

To reduce the collections of stones to a quantitative basis the following procedure was adopted. The lake shore was remodelled on a wooden tray 14×14 in., and the number of stones which fitted into this area was counted. The total number of stones in each collection being known, a quantitative basis was in this way arrived at. The trays were made 14×14 in. in area to allow for the overlap of the stones off the edges of the trays. The 14×14 in. was reckoned as 12×12 in.

In all types of collection the material was placed in buckets and taken up to the laboratory for examination. Before any conclusions were drawn, a very

large number of collections were made. Approximately sixty-five buckets of stones and sand were collected, the number of stones examined being roughly 600.

III. Environmental conditions.

These may be conveniently subdivided into:

(*a*) Physiographical and geological.

(*b*) Physical.

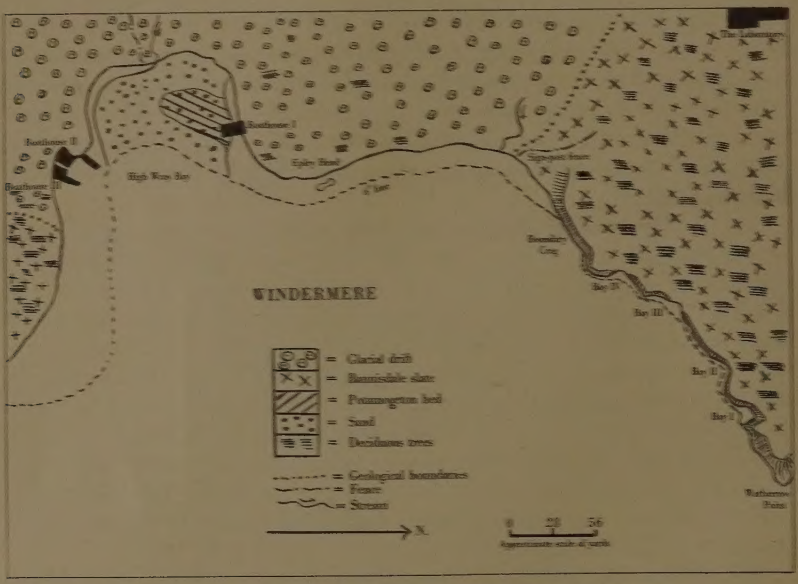


Fig. 1. Map showing the main features of Wray Bay, Windermere.

(*a*) *Physiographical and geological.*

The area studied was situated below the laboratory at Wray on the western shore of the north basin of Windermere (See Text-fig. 1 and Plate I); it included the shore between Boathouse III and Watbarrow Point. Collections were made along this shore from the water's edge to a depth of 2 m. All the depths given are reduced to the "normal water-level" of the lake, i.e. 129 ft. 9 in. O.D. This normal water-level was determined by a general inspection of the fringing vegetation. Continuous records of the water-level in the lake have not been taken for long enough to give a true "normal water-level."

From the ecological standpoint the advantages of this stretch of shore are very great, chiefly because it shows a gradient between two extreme types of

environment. From Watbarrow Point to Sign Post Fence the coastline is made up of a series of steep rocky headlands and stony bays, which are exposed to southerly gales. From Sign Post Fence to Epley Head the coastline is unbroken by bays or headlands, and the grass comes down to the water's edge. Also, this coastline is considerably sheltered from gales. Beyond Epley Head the coastline bends in to form High Wray Bay, which is very sheltered, and fringed with sand and shingle. Beyond High Wray Bay the coastline slopes out again to Boathouse III, becoming gradually more exposed, and increasingly rocky.

Actually the form of the coastline is entirely dependent on the geological formation. From Watbarrow Point to Sign Post Fence the shore is formed out of Bannisdale Slate and in future will be referred to as the Bannisdale Shore. The Bannisdale Slate is a hard, coarsely cleaved rock, and by virtue of its hardness resists erosion and gives rise to steeply sloping headlands.

The erosive stages in the course of the disintegration of these headlands are very important and exert a dominating influence on the composition of the animal population. Four stages may be distinguished:

(1) *Smooth rock face.* In this stage erosion has only produced a slight pitting of the surface, otherwise the rock is practically smooth.

(2) *Creviced rock face.* The smooth rock face is seamed by irregularly placed crevices, the crevices forming the boundaries of areas of smooth rock face.

(3) *Disintegrated rock face.* Crevices far more numerous, till the rock face is broken up by a system of anastomosing crevices.

(4) *Paved "fissure."* This actually represents the first stage in the formation of a bay. The crevicing of the rock has caused such weakening that large portions have been loosened and broken off, forming a narrow fissure paved by large slabs.

The four stages just mentioned are a perfectly graded series and can be seen at many places near Watbarrow Point. By virtue of the rudimentary cleavage which they possess, the Bannisdale Slates tend to weather into flat, smooth slabs. As the ruggedness of the Bannisdale Slate formation would not pay for the trouble of clearing with a view to pasture this formation has heavily wooded shores. From these woods a great quantity of vegetable detritus, sticks, leaves, etc., is derived, which collects under the boulders, and in the interstices of the gravel patches.

The remainder of the selected shoreline must now be considered. The geological formation is here Glacial Drift, and will be referred to as the Drift Shore. By virtue of its uncompacted state the Drift is far more easily eroded than the Bannisdale Slates. The matrix of sandy clay in which the characteristic rounded stones are embedded is washed away, leaving these stones behind to form a compact pavement. The stones, although rounded or at least sub-

angular owing to the erosive influence of the glacier which transported them, are not smooth but have rough and deeply pitted surfaces. In contrast to the Bannisdale formation the Drift is cleared of trees, being eminently suitable for pasture. From this pasture the amount of vegetable detritus which finds its way to the Drift Shore is small.

In the extreme corner of Wray Bay there is a third type of environment, in which the substratum is predominantly sandy. This is due to the fact that in this sheltered position wave action is at a minimum, and the sand eroded from the Glacial Drift is not washed away but settles to the bottom almost immediately. The result of this is to bury the stones beneath sand, and to coat heavily the surfaces of those which are left exposed. An examination of this part of the coast between Boathouse I and Boathouse II shows this process in all its stages. In the more exposed portions of the coastline the stones gradually become more scattered as the smaller intervening stones are covered, till finally only large isolated stones or clusters are to be seen, all of which are covered on the upper surfaces with sand. This is referred to as the Sand Shore. The shoreline investigated therefore changes, more or less gradually, from the exposed littoral of the Bannisdale formation to the quiet littoral of the Sand Shore, derived by erosion of the Glacial Drift formation; or to express this in another way, changes from a primitive shoreline in an early stage of erosion to an advanced shoreline in a later stage of erosion (Pearsall, 1921).

The composition of the rooted vegetation shows definite relations to the shoreline. The Bannisdale Shore shows only a sporadic growth of *Littorella* and *Lobelia*, which rarely extends upwards to less than 1 ft. of water. The Drift Shore, however, shows a very rich growth of *Littorella* and *Lobelia* extending to the lake edge in water so shallow that the plants are often exposed when the lake level falls below normal. The probable explanation of this difference in the vegetation is that the great quantities of sand derived from the erosion of the Drift form a suitable medium for the growth of *Littorella* and *Lobelia*, whereas the Bannisdale Shore yields little sediment and is therefore not so favourable to these plants. Furthermore the exposed character of the Bannisdale Shore prevents the plants extending into shallow water. The features of the portion of the shoreline under investigation and the relation of the submerged rooted vegetation to these features are summarised in the table below.

Table I. *Physiographical details of the littoral region.*

	Bannisdale Shore	Drift Shore	Sand Shore
(1)	Exposed	Fairly sheltered	Very sheltered
(2)	Flat, smooth stones	Rounded, rough stones	Stones absent or scattered
(3)	Heavily wooded	Pasture with occasional trees	Pasture with occasional trees
(4)	*Littorella* and *Lobelia*, sporadic	*Littorella* and *Lobelia*, ab.	*Littorella* and *Lobelia*, ab.

(*b*) *Physical.*

A number of physical factors which it was thought might influence the fauna were investigated, but by no means all of them could be successfully correlated with the composition of the fauna. In fact some of these physical factors, in the light of present knowledge, appear to have no influence in determining the character of the fauna. The factors investigated were: wave action, fluctuations in water-level, light, temperature, and dissolved oxygen.

(i) *Wave action.* This is probably the most important factor in determining the composition of the littoral fauna. It also affects to a considerable extent the shape of the animals living under its influence. The various types of shoreline described in the previous section are all the result of selective wave action, and the faunistic connections are extremely close. The erosive power of the waves was shown by the occurrence of stones with rounded corners and grooved surfaces. The action of the waves is clearly seen when the plant distribution is considered, the tendency being for plants to grow more abundantly in regions where the conditions are more tranquil and wave action less violent. Plants depend for their successful growth on the presence of a soft substratum to provide them with nutrient material and a firm rootage. Obviously wave action will tend to remove sediment, and therefore prevent extensive plant growth (Pearsall, 1921). The fact that it is the deposition of sediment that is important, and not merely wave action, is proved by the occurrence of a tuft of *Myriophyllum* on Watbarrow Point, one of the most exposed portions of the whole lake. Here a little deposition has taken place in a narrow crack and thus enabled the *Myriophyllum* to obtain a root hold, although exposed to considerable wave action. Regarding the shoreline purely from the point of view of plants in relation to sedimentation, it is noticeable that there is a steady increase in plant growth from Watbarrow Point to the corner of High Wray Bay. That is, the plants increase as more sheltered conditions are reached.

(ii) *Fluctuations in water-level.* The lake level in times of normal rainfall stands at 129 ft. 9 in. O.D. [see p. 10]. In times of flood it may rise to as much as 135 ft. O.D., and in times of drought is said to sink as low as 128 ft. O.D. The level may alter at a surprisingly rapid rate, 1 in. per hour being not unusual. The lake levels were read from a graduated post in the laboratory boathouse.

Work in progress (unpublished) on the migrations of the littoral fauna shows that fluctuations in level are an important factor in this zone.

(iii) *Light* was investigated but was found not to correlate in any way with the general distribution of the fauna.

(iv) *Temperature* changes appeared to have no marked influence on the fauna, the general composition of the fauna at any given place being the same in summer and winter alike.

(v) *Dissolved oxygen*. The results of a large number of estimations of dissolved oxygen showed that water in the area generally was adequately oxygenated. The maximum was 6·9 c.c./litre, while the minimum was 6·2 c.c./litre.

The records for light, temperature, and fluctuations in lake level are deposited with the Freshwater Biological Association of the British Empire, Wray Castle, Windermere.

IV. Food.

It is obvious that the nature of the shore might influence the food supply and so affect the composition of the fauna. In the later stages of the work considerable attention was therefore paid to the food of the animals living in the littoral region. The procedure adopted was to remove the gut of the animal as soon after capture as was possible, after which it was placed on a microscope slide and gently pressed by a cover-glass so as to squeeze out the contents. If the gut was too resistant to yield to this treatment the contents were actually dissected out, and examined under the 1/6 and 1/12 in. objectives.

Many of the animals, particularly the insect larvae and nymphs, were found to have been feeding on the slimy growth which covers the surfaces of the boulders. This slimy growth consists of a tangled felt of algal threads, in which small particles of quartz and other mineral matter have become entangled. Growing with this felt are a large number of Diatoms, while living amongst it are a number of Ostracods and Copepods. In the gut contents it is possible to distinguish the remains of the algal filaments and Diatoms, while the mineral particles remain of course untouched. When a fresh slide of this slimy growth is compared with the gut contents of an animal, the similarity between the two samples is unmistakable.

Another type of food was small particles of wood or plant fragments, and small pieces of dead leaves. Also of fairly common occurrence were animals feeding on a detritus of mixed origin, both organic and inorganic, which forms part of the substratum of the lake where wave action does not prevent its deposition. These are referred to as detrital feeders, in contrast with the animals feeding on the slimy covering of the rocks, which are referred to as the felt feeders.

Below (Table II) is given a list of the food of a number of littoral animals.

This list shows the importance of the algal felt as a food material. By far the greater number of the animals live on this substance, carnivores being the exception rather than the rule in the region investigated. Important points arise in connection with this algal felt. It probably shows seasonal fluctuations in amount, and this may affect the numbers of animals present at any given time. It may be possible to correlate the area available for growth of the algal felt with the density of the fauna in a particular area, but no data are at present available. Another important consideration is to what extent

the deposition of sand affects the felt, and thereby influences those members of the fauna which subsist upon the felt. It seems almost certain that a layer of sand would inhibit the growth of the felt. Further investigations are being made on this point.

Table II. *Gut contents of a number of littoral animals.*

Unless otherwise stated, at least ten individuals of each animal were examined.

Species	Food	Remarks
Ecdyonurus venosus	Algal felt	
Centroptilum sp. ?	Algal felt	Contained Sporozoa
Nemura sp. ?	Insect remains	Five specimens examined
Tinodes sp. ?	Algal felt	
Polycentropus flavomaculus	Small Crustacea	
Limnophilius politus	Algal felt + wood fragments	
Stenophylax infumatus	Wood fragments	
Mystacides nigra	Algal felt	
Sericostoma personatum	Algal felt + Littorella fragments	In one individual remains of an insect larva were found
Lepidostoma hirtum	Algal felt + wood fragments	
Agapetus sp. ?	?	Gut full of a gelatinous mass. At the *edges* this could be seen breaking up into flagellate bodies
Gammarus pulex	Fine "mush," gut contents indistinguishable	Probably a scavenger
Asellus meridianus	Felt + detritus	
Tipulid larvae	Carnivorous	Rich Flagellate fauna. A few Ciliates in the gut
Chironomus sp. ?	Detritus	
Platambus maculatus	Insect remains	One individual only
Cnemidotus impressus	Plant débris (?)	One individual only
Ancylus fluviatilis	Felt	
Limnaea peregra	Felt	
Stylaria lacustris	Felt	
Limnodrilius sp.	Detritus	
Bdellocephala punctata Polycelis nigra Dendrocoelum lacteum Planaria lugubris	Fine "mush," gut contents indistinguishable	Scavengers ?

V. The fauna.

Before considering the actual distribution of the fauna it is necessary to point out that it shows a distinct periodicity throughout the summer months. During the summer certain insect larvae were temporarily absent from the "exposed littoral," and certain other invertebrates were represented only by cocoons or eggs. When engaged on any sort of ecological work in the littoral region it is essential to bear this fact in mind. Actually the time of year when the fauna is most fully represented is November to February.

In the course of the work it was noted repeatedly how the fauna was controlled by the physiography of the shoreline. As soon as any modification was

produced by erosive forces upon the shoreline, the modification reacted upon the fauna by eliminating one form or admitting another. As pointed out earlier on, this single stretch of shoreline shows in miniature the change from "Primitive" to "Advanced" conditions. With this physiographical basis in mind, the main types of shoreline and their associated faunas will be considered and contrasted.

A. *The Bannisdale Shore.*

(1) *The vertical rock faces.*

A description of the erosion stages of these rock surfaces was given earlier in this paper. It is now necessary to consider the fauna associated with these changes. The results obtained by collecting in early July are recorded in Table III. The numbers given are based on a single sample at each habitat. These figures were confirmed by another collection two weeks later. In the spring of this year these figures were again confirmed.

Table III. *Fauna of vertical rock faces on Bannisdale Shore.*

Erosion stage	Depth	Population per square foot	
"Smooth" rock face, e.g. Watbarrow Point	0–2 ft.	Ancylus fluviatilis	80
		Limnaea peregra	1
↓		Tinodes (below 2 ft.)	10
"Creviced" rock face, e.g. Watbarrow Point	0–2 ft.	Ancylus fluviatilis	50
		Limnaea peregra	1
—		Tinodes sp.	5
↓		Leptocerus bilineatus	15
"Disintegrated" rock face, e.g. Boundary Crag	0–2 ft.	Ancylus fluviatilis	50
		Limnaea peregra	3
—		Tinodes sp. (below 2 ft.)	10
—		Leptocerus bilineatus	5
—		Mystacides nigra	7
—		Polycelis nigra	Scarce
—		Rhabdocoelida	Scarce
↓		Centroptilum luteolum	Scarce
"Paved" fissure, e.g. between Boundary Crag and Bay IV	0–6 in. (below 6 in. these fissures pass into the smooth rock face)	Ancylus fluviatilis	20
		Limnaea peregra	6
		Leptocerus bilineatus	8
		Mystacides nigra	24
		Polycelis nigra	14
		Oecetis lacustris	1
		Planaria lugubris	12
		Ecdyonurus venosus	4
		Piscicola geometrica	2
		Sida crystallina	2

Arrows indicate the direction in which erosion is proceeding.

Several points emerge from this table, the most important of which is that the advance in erosion is paralleled by an increase in numbers of the fauna. The factor at work is probably shelter; it was very noticeable how the caddis larvae tended to rest with their cases lengthwise in the crevices. This was particularly true of pupating *Leptocerus bilineatus*. Secondly, as the habitat becomes less specialised the numbers of the individuals decrease, while the number of different species increases. For example, on the "smooth" rock

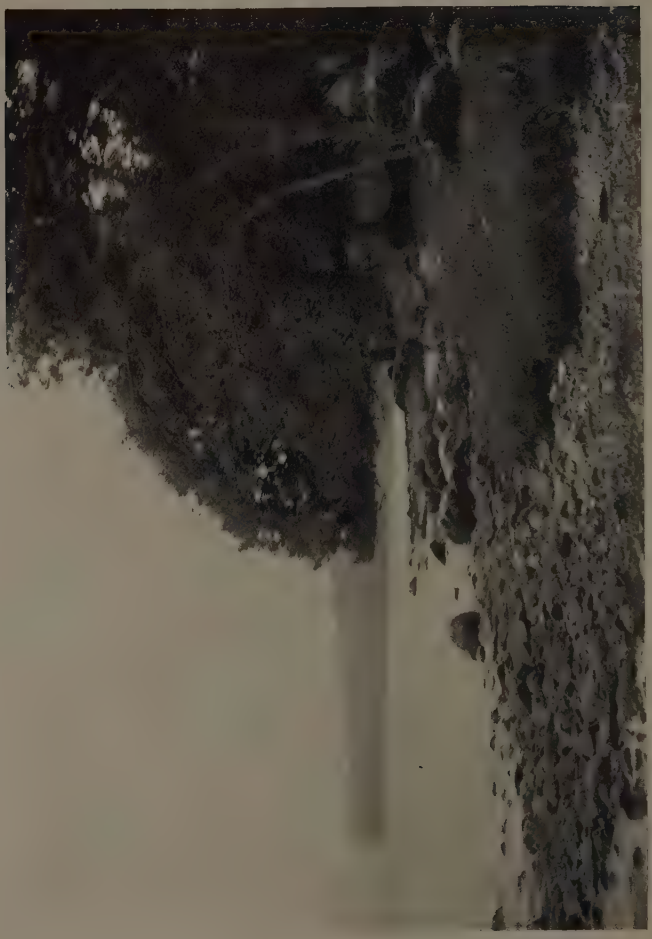
Table IV. *Fauna of stone shore, Bannisdale Shore.*

	Bay I (12. vii. 32)		Bay III (5. vii. 32)				Bay III (27. viii. 32)		Bay IV (26. viii. 32)
Depth ...	2 ft.	3–5 ft.	Lake edge	1 ft. Stones	1 ft. Shingle	2–3 ft.	2½ ft. *Lobelia Littorella*	4–5 ft.	Lake edge
Mystacides azuraea	.	.	.	1	.	.	.	.	.
Leptocerus bilineatus	15	.	2	.	6	3	9	10	1
Sericostoma personatus	27	1	.	.	7	.	5	3	.
Stenophylax nigricornis	2	.	.	.	.	.	.	5	1
Mystacides nigra	.	8	.	2	.	7	.	10	2
Limnophilius politus	.	2	.	.	.	.	.	.	2
Oecetis lacustris	10	12	.	.	.	.	1	5	.
Tinodes	.	2+(pupae)	1	3	.	1	.	2	.
Lepidostoma hirtum	.	.	.	.	.	.	3	.	.
Polycentropus flavomaculus	.	3	.	1	2	3	.	2	15
Ancylus fluviatilis	2	11	.	51	1	15	.	Present	.
Limnaea peregra	1	3	.	.	.	1	21	.	.
Pisidium sp.	1	.	.	.	.	.	2	1	.
Sphaerium sp.	1	.	.	.	.	.	.	.	.
Planorbis contortus	1	.	.	.	.	.	1	.	.
Gammarus pulex	14	.	.	.	11	.	4	2	1
Asellus sp.	.	.	.	1	.	.	.	.	4
Sida crystallina	1	.	.	2	.	.	.	.	.
Eisienella tetrahedra	.	.	4	.	.	.	.	.	.
Limnodrilius sp.	3	.	.	.	.	.	1	.	.
Helodrilius sp.	.	.	.	.	.	.	8	.	.
Glossisiphonia complanata	1	.	.	.	.	.	.	.	.
Nematode	1	.	.	.	.	.	1	.	.
Metriocnemus cubitalis sp.	.	.	.	50	4	8	.	7	.
Tanypus	.	3	.	1	1	.	.	.	.
Chironomus sp.	.	3	.	1	.	4	1	.	5
Hygrobatid mite	.	1	.	.	.	1	.	.	1
Sialis lutraria	.	1	.	.	.	.	.	.	.
Elmid larva	.	1	.	.	.	.	.	.	.
Platambus maculatus	.	.	2	.	.	.	.	.	.
Hydroporus palustris	.	.	1	.	.	.	.	.	.
Ecdyonurus venosus	.	.	.	1	7	2	.	1	.
Centroptilum sp.	.	.	.	.	.	.	.	.	1
Leuctra sp.	.	.	.	.	.	.	.	.	5
Sigara sp.	.	.	.	1	.	.	.	.	.
Polycelis nigra	.	.	.	1	.	.	.	.	.
Planaria lugubris	.	.	.	1	.	.	.	1	.
Planarian cocoons	.	.	.	Present	.	.	.	.	.
Ephydatia colonies	.	.	.	.	.	.	.	3	.
Total per sq. ft.	80	51	10	117	39	45	57	52	38

Table V. *Fauna of Drift Shore.*

	Sign Post Fence (7. vii. 32)			Epley Head			S. of Boat-house III
Depth ...	6 in.	3–4 ft.	Single large boulder 3–4 ft.	(26. vii. 32) 1 ft.	N.E. of Head (31. viii. 32) 6 in.	S.W. of Head (12. viii. 32) 2–3 ft.	(9. vii. 32) 2 ft.
			Base area = 12 × 6 in. Height = 6 in.		+ *Littorella*	Stones with *Fontinalis* and *Chaetopteryx*	A little *Myrio-phyllum*
Leptocerus sp.	1	.	.	.	.	1	.
Leptocerus bilineatus	.	17	23	33	8	3	.
Mystacides nigra	.	2	.	6	.	.	.
Tinodes + pupae	6	28	32	4	.	.	25
Agapetus sp.	.	1	.	.	.	.	
Polycentropus flavomaculus	.	.	4	7	.	.	.
Stenophylax nigricornis	.	.	.	2	.	1	1
Sericostoma personatum	.	.	.	.	1	.	.
Silo nigricornis	.	.	.	.	5	1	.
Stactobia fusicornis	.	.	.	.	2	.	.
Leptocerus excisus	.	.	.	.	.	1	.
Oecetis lacustris	.	.	.	.	.	2	1
Metriocnemus cubitalis sp.	.	2	13	.	.	.	15
Chironomus sp.	.	3	1	.	.	.	4
Ceratopogon sp.	.	.	.	.	2	1	.
Limnaea peregra	.	.	.	2	4	.	.
Ancylus fluviatilis	.	8	7	.	.	.	2
Ancylus cocoons	.	.	Present	33	.	.	.
Planorbis contortus	.	.	.	.	6	.	.
Planorbis albus	.	.	.		2	.	.
Sphaerium	.	.	.		1	.	.
Planaria lugubris	.	2	.	.	.	4	2
Bdellocephala punctata	.	1	.	.	.	.	3
Polycelis nigra	.	.	.	.	.	2	18
Planarian cocoons	.	.	Present	.	.	.	Present
Strongylosoma radiatum	.	.	1	.	.	.	.
Dendrocoelum lacteum	.	.	.	.	.	.	1
Herpobdella octoculata	.	.	.	.	1	.	.
Herpobdella atomaria	.	1		.	1	8	.
Piscicola geometrica	.	.	.	1	.	.	.
Glossisiphonia complanata	.	.	.	.	1	.	.
Helobdella stagnalis	.	.	.	.	.	2	.
Haemopsis sanguisuga	.	.	.	.	.	1	.
Glossisiphonia heteroclita	.	.	.		.	.	.
Leech cocoons	.	.	Present	.	.	.	.
Spongilla	.	.	3	.	.	.	.
Ecdyonorus venosus	9	.	.	20	.	.	.
Ephemera danica	.	.	.	.	1	.	.
Centroptilum	.	.	.	.	.	.	2
Gammarus pulex	.	.	.	1	6	6	Present
Elmid larva	.	.	.	1	.	1	.
Leuctra sp.	.	.	.	7	.	.	1
Nemura sp.	.	.	.	2	.	.	.
Chloroperla sp.	.	.	.	.	.	1	.
Eisienella tetrahedra	.	.	.	.	4	.	.
Helodrilius sp.	.	.	.	.	4	.	.
Hygrobatid mite	.	.	.	.	.	Common	3
Egg mass of Thyas venusta	.	.	.	.	.	.	Common
Sigara	5	.	.	.	.	.	21
Lacinularia socialis	.	.	.	.	.	.	Colonies common
Asellus sp.	.	.	.	.	.	.	1
Nais blanci	.	.	.	.	.	.	1
Hydropsychid egg mass	.	.	1	.	.	.	.
Tanypid egg mass	1	.	.	.	.	.	.
Limnodrilius	.	.	.	.	10	.	.
Egg mass of Limnaea peregra	.	.	Present	.	.	.	
Total per sq. ft.	22	65	85	119	59	35	101

surface there are eighty *Ancylus fluviatilis* to the square foot and two species of other invertebrates, while in the "paved" fissures there are only twenty to the square foot, but eight species of other invertebrates.



View of the drift type of boulder shore, Sign Post Fence. Taken at a period of low lake level.

MOON—FAUNA OF LAKE WINDERMERE

Face p. 19

(2) *The stone shore.*

Table IV shows nine representative collections from the stone shore. In Table IV each vertical column represents a single sample, from a particular depth. The samples were selected from the whole series of collections as being illustrative of the points raised in the text. The total number of collections made on the stone shore was forty-two. The complete list of this and other collections is deposited for reference at the Laboratory of the Freshwater Biological Association, Windermere.

B. *The Drift Shore.*

Since a discussion of the Bannisdale Stone shoreline involves numerous comparisons with the Drift Stone shoreline, it will be more convenient to pass straight on to the tables of the fauna of the Drift Shore. Table V shows seven collections from the Drift Shore. Altogether sixty-eight collections were made.

It is now possible to contrast the Bannisdale and Drift shorelines and see how far the fauna can be correlated with the environment. An examination of the complete series of collections showed that certain animals were more abundant on one type of shoreline than on the other. Table VI shows the result of this comparison. It is based on averages obtained from forty-two collections on the Bannisdale Shore, and sixty-eight on the Drift Shore.

Table VI. *Comparison of certain species on Bannisdale and Drift Shores.*

Species	Average population per sq. ft.	
	Drift Shore	Bannisdale Shore
Ancylus fluviatilis	8	29
Asellus sp.	1*	3
Leptocerus bilineatus	9	5
Chironomus sp. (Red "plumosus" type)	3*	5
Tinodes sp.	13	1
Ecdyonurus venosus	6	3
Sigara minutissima	8	1

* Found only where terrestrial detritus occurred, in a few localised areas of the Drift Shore.

In the absence of direct experimental work it would be rash to state definitely the factors responsible for this distribution. It is, however, possible to make certain tentative suggestions. *Ancylus fluviatilis* is far more abundant on the Bannisdale than on the Drift Shore. A possible reason for this may lie in the fact that *Ancylus* is unable to maintain itself amongst the abundance of other species which occur. A possible reason for the abundance of *Chironomus* ("*plumosus*" type) and *Asellus* can be found in the heavily wooded nature of the Bannisdale Slate formation. As pointed out earlier in this paper, the vegetable detritus collects under the stones on the Bannisdale Shore, forming a micro-habitat within the major habitat of the Bannisdale Shore. In this

micro-habitat wave action is prevented by the overlying stones and a condition of quiescence and decay is produced, much as in the ordinary pond. This condition is the natural one for *Chironomus* and *Asellus*, and possibly explains their greater abundance on the tree-backed Bannisdale Shore than on the Drift Shore. The greater abundance of *Ecdyonurus* may be correlated with the rougher surfaces of the stones on the Drift Shore, which enables the creature to wedge the spinous projections of its legs into the irregularities and so obtain a better grip. *Leptocerus*, *Tinodes*, and *Sigara minutissima* are animals which would obviously benefit by sheltered conditions, and this probably accounts for their distribution.

There are certain forms which are limited to one or other of the two shorelines. The names of these are given below, the numbers being averages based on sixty-eight collections from the Drift Shore and forty-two from the Bannisdale Shore.

Drift Shore	No. per sq. ft.	Bannisdale Shore	No. per sq. ft.
Coenis sp.	1	Sialis lutraria	1
Eisienella tetrahedra	2	Limnophilius rhombicus	5
Helodrilius sp.	4		
Ephemera danica	2		
Silo nigricornis	5		
Agapetus sp.	1		
Herpobdella atomaria	6		
Leuctra sp.	3		
Centroptilum sp.	6		

In this case it seems reasonable to suppose that the Oligochaeta *Helodrilius* and *Eisienella tetrahedra*, and the nymphs of *Ephemera danica* benefit by the quantity of sand on the Drift Shore, which forms a favourable medium for their burrowing operations. The presence of *Agapetus* and *Silo nigricornis* may also be influenced by sand, for both these caddises build their cases of a grade of mineral which is common on the Drift Shore, but sparse on the Bannisdale. *Coenis*, *Leuctra*, and *Centroptilum* are probably favoured by the more sheltered conditions.

The great abundance of *Herpobdella atomaria* and leeches in general on the Drift Shore is of considerable interest, because it is probably correlated with the great abundance of *Planorbis* and *Valvata* here. These two Gastropods feed on the *Littorella* and *Lobelia*, which are abundant along the Drift Shore owing to deposition of sand washed from the drift. As Gastropods are the staple diet of leeches, it is reasonable to correlate the abundance of leeches with the Gastropods. Correlating the physiography with the biology, the following scheme could be constructed:

Glacial Drift —EROSION→ Sand —DEPOSITION→ *Littorella* / *Lobelia* → *Valvata* / *Planorbis* → *Herpobdella atomaria.*

Sialis and *Limnophilius politus* are almost exclusively confined to the Bannisdale Shore, and *Sialis* in particular is interesting: it is pre-eminently a

creature of the Quiet Littoral at depths where wave action has little influence, and its occurrence under exposed littoral stones is unusual. It is probably to be connected with the same factors producing the micro-habitat already mentioned, in which *Chironomus* and *Asellus* are found. *Limnophilius politus*, a caddis building its case of regularly cut wood fragments, would encounter far more building material on the Bannisdale Shore than on the Drift Shore, a fact which may control its distribution.

In two collections made in Bay III, one from large boulders and the other from coarse shingle, there were certain indications as to the possible effect on the fauna of the relative stability of the substratum. On the shingle *Ancylus*, *Polycentropus* and *Tinodes* were absent and *Metriocnemus cubitalis* decreased as compared with the numbers living on large boulders. There was, however, an increase in the number of *Ecdyonurus* and *Gammarus* on the shingle. These contrasts in animal population are probably due to the fact that *Polycentropus*, *Tinodes*, *Ancylus* and *Metriocnemus cubitalis* are all either tube builders or clinging organisms which require a stable foundation. *Gammarus* and *Ecdyonurus*, on the other hand, are active swimmers and could survive in shifting shingle.

C. *The Sand Shore.*

Tables VII, VIII and IX show collections from the Sand Shore. Each vertical column represents a single sample from each depth. The total number of collections was twenty-one.

Table VII shows the type of fauna found on the sandy shore, and the influence of various kinds of substrata on the animals.

Table VIII shows that with increase in the numbers of stones there is an increase in the number of species present. The stones represent a less specialised habitat than the bare sand.

Table IX shows the influence of vegetation on the fauna.

In a consideration of the faunal trends on the Sand Shoreline the outstanding fact is that all forms which require a solid substratum tend to be eliminated, their place being taken by burrowing forms. Such forms, for example, as *Ancylus*, *Limnaea*, *Ecdyonurus*, and *Leuctra* are absent, except where isolated boulders are found. Caddises such as *Mystacides nigra*, which are dependent on wood fragments and débris for the construction of their cases, are absent on bare sand. There is, however, a great increase in burrowing forms such as *Chironomids*, the Oligochaete *Limnodrilius*, and the Mollusc *Pisidium* which progresses through the sand with its plough-like foot. The influence of the micro-habitat is again seen in the occurrence of *Chironomus* ("*plumosus*" type) and *Asellus* under boulders where large quantities of decaying vegetable matter have accumulated.

Another point clearly illustrated by collections from the Sand Shore was the influence of vegetation. This can be clearly seen when Table IX, showing

vegetational effects on the bare sand, is consulted. The general effect of a thick growth of vegetation is to increase the number of Hygrobatid Mites and Gastropod Molluscs, and at the same time to introduce species which are rarely found except in association with vegetation; as for example *Phrygaenea grandis* or *Physa fontinalis*. The increase in Hygrobatid Mites is probably to be correlated with the extra shelter afforded to these small creatures by a dense interlacing vegetation, while presumably food supply explains the presence of the Gastropods. It is further noticeable that the erect Potamogeton type of vegetation shows a greater number of new forms when compared with bare sand, than do the "sward" growths of *Lobelia*, *Littorella* or *Isoetes*.

Table VII. *Fauna of the Sand Shore, July 19th*, 1932.

Depth:	2 ft. Stones resting on vegetable detritus	2 ft. Sand, scattered pebbles and Isoetes	6 in. Coarse shingle, sand and plant detritus	2 ft. Bare sand, a little mud and much plant detritus
Metriocnemus cubitalis	.	.	3	.
Chironomid	.	.	13	250
Tanypus sp.	.	.	1	.
Ceratopogon sp.	.	.	.	1
Metriocnemus sp.	1	3	.	3
Chironomus ("plumosus" type)	28	18	.	.
Leptocerus bilineatus	28	4	3	8
Stenophylax nigricornis	.	.	3	.
Sericostoma personatum	3	.	8	.
Silo nigricornis	1	8	4	.
Mystacides nigra	35	2	.	.
Oecetis lacustris	12	.	.	.
Centroptilum sp.	.	1	1	.
Gammarus pulex	3	3	12	.
Ancylus fluviatilis	3	.	2	.
Sphaerium sp.	.	.	2	.
Pisidium sp.	5	7	.	50
Limnodrilius sp.	2	20	18	3
Helodrilius sp.	.	.	2	.
Glossisiphonia complanata	5	.	1	.
Glossisiphonia heteroclita	1	.	4	.
Helobdella stagnalis	1		1	.
Piscicola geometrica	1	.	.	.
Cocoons-Eisienella tetrahedra	.	16	.	.
Isopteryx sp.	.	.	1	.
Sialis lutraria	2	.	.	.
Sigara sp.	1	1	.	.
Tinodes	.	1	.	.
Herpobdella atomaria	3	.	.	.
Total per sq. ft.	135	84	79	315

An observation was made on the small red *Chironomids* that are so abundant on the Sand Shore, and which may represent an adaptation to life in an unstable medium such as sand. These Chironomids, as soon as the dish containing them was agitated, at once coiled up into circles, and remained so until the water had ceased moving. Possibly this coiled position is advantageous to the animal when living in an uncompacted substratum liable to mechanical disturbance.

Table VIII. *Fauna of Sand Shore. Collection between Boathouses I and II, July 19th, 1932.*

Depth:	2 ft. Bare sand	2 ft. Isolated stones	2 ft. Clusters of stones
Pisidium sp.	35	1	1
Chironomid	43	.	.
Silo nigricornis	3	.	
Sericostoma personatum	2	.	4
Ephemera danica	2	.	.
Limnodrilius sp.	1	.	.
Hygrobatid mite	1	.	.
Eisienella tetrahedra	1	.	.
Elmid larva	1	.	.
Sigara sp.	1	.	1
Haemopsis sanguisuga	.	1	1
Glossisiphonia complanata	.	1	.
Helobdella stagnalis	.	2	1
Planorbis spirorbis	.	1	.
Ancylus fluviatilis	.	2	3
Ecdyonorus venosus	.	1	2
Gammarus pulex	.	6	11
Bdellocephala punctata	.	1	.
Tanypus sp.	.	1	3
Limnaea peregra	.	1	.
Lacinularia socialis	.	Several colonies	.
Leptocerus bilineatus	4	.	14
Mystacides nigra	.	.	5
Polycentropus flavomaculus	.	.	2
Planaria lugubris	.	.	1
Asellus sp.	.	.	1
Piscicola geometrica	.	.	2
Herpobdella atomaria	.	.	1
Herpobdella octoculata	.	.	3
Glossisiphonia heteroclita	.	.	2
Tinodes	.	.	Present
Total per sq. ft.	94	18	58
Number of different species	11	12	19

VI. Discussion and conclusions.

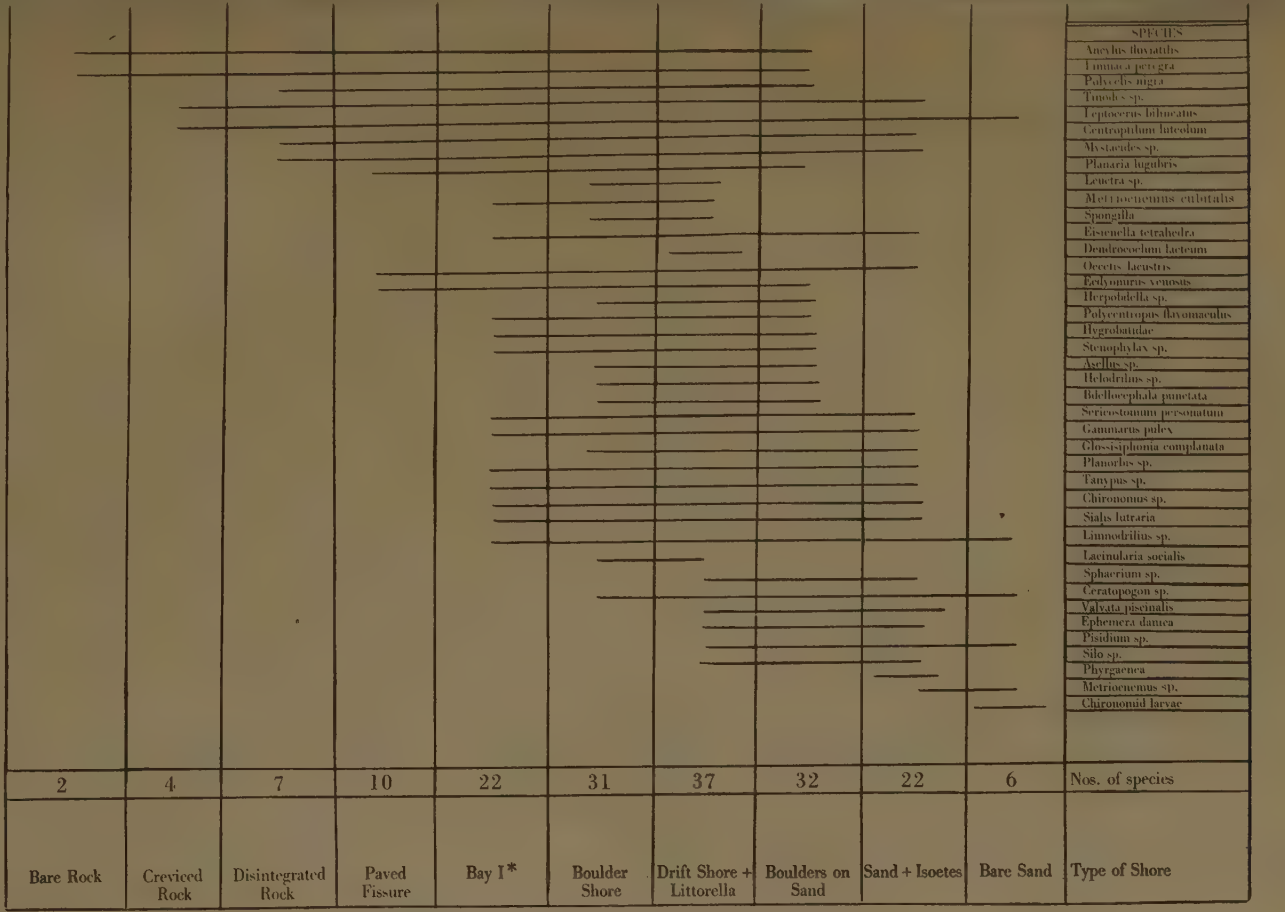
A definite attempt has been made to correlate the fauna with the physiographical features of a portion of the shoreline of Windermere and to find out how far changes in the physiography are reflected in the fauna. It now remains to be seen whether any conclusions can be made concerning the fauna, when the shoreline is viewed as a whole, and not in a number of separate sections. As the work stands at present it is only possible to make generalisations, and to regard them as tendencies rather than hard-and-fast rules, since any hard-and-fast rule applied to an animal community is bound to meet with disaster.

The stretch of shoreline under investigation grades from bare rock face into sand, with an intervening area of stone shoreline; or in other words it represents the transition from "Primitive" to "Advanced" conditions. When all the collections are examined it is seen that on the bare rock face, and the bare sand, there are large numbers of a few species, while on the stony areas there are fewer individuals per species, but a great increase in the number of

Table IX. *Fauna of Sand Shore, July 19th*, 1932.

	Depth: 2 ft.	4 ft.	4–6 ft.
	Bare sand	Sand with *Littorella* and *Isoetes*	Sand with *Potamogeton lacustris*; *Sparganium minimum*; *Elodea canadensis*
Pisidium sp.	50	4	.
Chironomid	250	.	20
Metriocnemus sp.	6	Present	.
Leptocerus bilineatus	8	30	20
Limnodrilius sp.	3	7	.
Ceratopogon sp.	1	2	.
Chironomus sp.	.	8	4
Leptocerus excisus	.	5	.
Ephemera danica	.	1	.
Sialis lutraria	.	3	6
Tanypus sp.	.	1	.
Hydroptila sp.	.	1	.
Oecetis lacustris	.	1	3
Sericostoma personatum	.	2	.
Nemura sp.	.	2	.
Silo nigricornis	.	1	.
Phrygaenea grandis	.	1	4
Glossisiphonia complanata	.	1	.
Planorbis contortus	.	2	.
Gammarus pulex	.	1	.
Hygrobatid mite	.	.	23
Oxyethira sp.	.	.	1
Lepidostoma hirtum	.	.	21
Stactobia fusicornis	.	.	1
Oecetis furva	.	.	1
Mystacides nigra	.	.	1
Valvata piscinalis	.	.	24
Physa fontinalis	.	.	20
Piscicola geometrica	.	.	2
Planorbis crista	.	.	36
Asellus sp.	.	.	1
Amphinemura sp.	.	.	1
Herpobdella atomaria	.	.	5
Limnaea peregra	.	.	15
Limnocharid mites	.	.	10
Total individuals per sq. ft.	318	73	219
Total number of species	6	19	21
Total number more species as compared with previous column	.	14	15

different species present. What this means is that the two extremes of the environmental series both necessitate considerable adaptation and specialisation in any animals living there. Bare sand is just as specialised a habitat as bare rock, and only a few forms can live there. Intervening between the two extremes of bare sand and rock is the stone shore. The stone shore is an extremely mixed environment, the stones being of all sizes and shapes, and embedded in every type of matrix. Their upper surfaces are exposed, their sides less so, while their under surfaces are sheltered and here accumulation of material takes place. Furthermore they are cracked, pitted, and split in every conceivable manner. This means that many animal forms can find some niche in the environment where it is possible to live. What it amounts to is that the stone shoreline constitutes a major environment which is built up out



* Bay I is transitional between a true bay and a paved fissure.

Fig. 2. Diagram showing the distribution of the principal members of the littoral fauna.

of innumerable smaller environments or "micro-habitats." Each part of a stone or patch of shingle and sand represents a micro-habitat providing special life conditions of its own. Since no one stone or patch of shingle and sand is quite the same as another, it means that there are environments or habitats suitable for a much greater number of species than on bare sand or rock. If Table VIII is consulted it will be seen that as the number of stones increases, so does the number of different species of animals normally characteristic of the stone shoreline. Consequently it seems reasonable to suppose that the increase in the number of stone shore species amongst stones on a sand shore is due to the fact that the stones provide a number of micro-habitats within the major-habitat, so that lack of specialisation is no longer a disadvantage to the animal.

The influence of vegetation is felt wherever it occurs on the shoreline. Nor need the growth of vegetation be excessive in order to produce an effect, for in one case an isolated tuft of *Myriophyllum* was sufficient to increase the population of Hygrobatid Mites. Vegetation adds an additional number of possible habitats or environments to those already existing within the major-habitat (Table IX). Hence the appearance of new species, and the increase in the total population wherever a growth of vegetation occurs.

Although suggestions have been made for the distribution of certain forms, there are other members of the fauna whose distribution is obscure, and the reasons for it still more so. Examples are *Gammarus pulex*, *Sericostoma personatum*, *Lacinularia socialis*, *Spongilla* or the larva of *Elmis*.

Regarding the littoral region as a whole, it is interesting to note that the total number of species recorded is eighty-nine, a figure which agrees fairly closely with that given by Elton for the average of the total number of species found in different types of habitat (Elton, 1933).

VII. Summary.

1. A quantitative estimation was made of the littoral fauna of a lake shore, and the fauna was correlated with the physiography.

2. The most important physical factors in the littoral region are wave action and fluctuation in lake level. The important features of the physiography depend on the relatively greater resistance to erosion of the Bannisdale Slates which compose part of the area, than the Glacial Drift which composes the remainder. The various stages in the erosion of the coastline are considered in detail, and it is shown how there is a graded series from a "Primitive" to an "Advanced" type of lake shore.

3. The food of littoral animals consists in most cases of the slime covering the submerged boulders. This slime consists of a felt of algal filaments, in which mineral matter and various organisms become entangled. Carnivores are exceptional.

4. The fauna in each type of environment is described and a number of sample tables are given. The main points are:

(*a*) Close correlation in many cases between fauna and physiography.

(*b*) The existence of a number of micro-habitats within the main or major habitat.

(*c*) That specialised environments have fewer species than a generalised habitat, but the number of individuals of any species per unit area is greater.

(*d*) Vegetation increases the number of certain species and also shelters species not found elsewhere in the littoral region.

5. Total number of recorded species inhabiting the littoral region is eighty-nine.

VIII. Acknowledgments.

My thanks are due to Mr Ullyott of Trinity College, Cambridge, for assistance in the arrangement of the paper; and to Dr W. H. Pearsall of Leeds and Mr J. T. Saunders of Cambridge, for reading through the manuscript.

APPENDIX.

List of fauna.

July 1st to September 14th, 1932.

Examples of most of these forms are deposited at the Laboratory of the Freshwater Biological Association, Windermere. Since this investigation was concerned only with the larger members of the fauna, the following list does not include a few small species of *Entomostraca* which occur.

PORIFERA.

Spongilla lacustris (A[1]) (Lin.)
Spongilla fragilis (A) (Leidy)

PLATYHELMINTHES.

Tricladida.

Planaria lugubris (A) (O. Schm.)
Polycelis nigra (A) (Ehrenb.)
Dendrocoelum lacteum (A) (Müll.)
Bdellocephala punctata (A) (Pallas)

Rhabdocelida.

Strongylosoma radiatum (A) (Müll.)
(One unidentified species (A).)

ROTIFERA.

Lacinularia socialis (A) (Ehrenb.)
Rotifer sp. (A) (Schrank)

NEMATODA.

Several unidentified species (A).

ANNELIDA.

Oligochaeta.

Limnodrilius sp. (A) (Claparede)
Nais blanci (A) (Piguet)
Eisienella tetrahedra (A) (Say.)

Annelida (*cont.*).

Helodrilius sp. (A) (Hoffm.)
Chaetogaster sp. (A) (K. Baer)
Stylaria lacustris (A) (Lin.)

Hirudinea.

Herpobdella atomaria (A) (Carena)
Herpobdella octoculata (A) (Lin.)
Helobdella stagnalis (A) (Lin.)
Glossisiphonia complanata (A) (Lin.)
Haemopsis sanguisuga (A) (Lin.)
Piscicola geometrica (A) (Lin.)
Glossisiphonia heteroclita (A) (Lin.)

ARTHROPODA.

Crustacea.

Sida crystallina (A) (Müll.)
Asellus sp. (Meridiane?) (Racovitza)
Gammarus pulex (A) (Lin.)

Insecta.

Plecoptera.

Leuctra sp. (Stephens)
Nemura sp. (Latr.)
Chloroperla sp. (Newm.)
Amphinemura sp. (O.L.)
Isopteryx (?) sp. (Pictet)

[1] A = adult.

HEMIPTERA.

Gerris najas (A) (De G.) (inside boat-houses only)
Sigara minutissima (A) (Lin.)

NEUROPTERA.

Ecdyonurus venosus (Fab.)
Centroptilum luteolum
Coenis sp. (Stephens)
Ephemera danica (Müll.)
Sisyra sp. (Burm.)
Sialis lutraria (Lin.)
Tinodes sp. (McLachl.)
Polycentropus flavomaculus (Pictet)

TRICHOPTERA.[1]

Leptocerus bilineatus (Lin.)
Leptocerus excisus (Mort.)
Leptocerus sp. (Leach)
Oecetis lacustris (Pictet)
Mystacides nigra (Lin.)
Stenophylax nigricornis (Pictet)
Stenophylax infumatus (McLachl.)
Silo nigricornis (Pictet)
Silo pallipes (Fab.)
Sericostoma personatum (McLachl.)
Agapetus sp. (Curt.)
Stactobia fusicornis (Schneid.)
Hydroptila sp. (Dalm.)
Setodes sp. (Ramb.)
Limnophilius politus (McLachl.)
Phrygaenea grandis (Lin.)
Neuronia sp. (Leach)
Lepidostoma hirtum (Fab.)

COLEOPTERA.

Platambus maculatus (A) (Lin.)
Hydroporus palustris (A) (Lin.)
Cnemidotus impressus (A) (Pz.)
Gyrinus sp. (Geoff.) (in boathouses only)

COLEOPTERA (*cont.*).

Elmis sp. (A) (Lat.)
Hydraena gracilis (A) (Germ.)
Haliplus sp. (Lat.)
Elmis sp. (Lat.)
Parnid sp.

DIPTERA.

Hyphydrus ferrugineus (Lin.)
Chironomus sp. (Meigen)
Corynonenura sp. (Winnertz)
Metriocnemus sp. (Van de Wulp.)
Tanypus sp. (Meigen)
Chironomids
Metriocnemus cubitalis (Kieff)
Tipulid sp.
Ceratopogon sp. (Meigen)

Arachnida.

HYDRACARINA.

Thyas venusta (A) (C. L. Koch)
Hygrobatidae (A) (several species)
Limnocharidae (A) (several species)

MOLLUSCA.

Gastropoda.

Ancylus fluviatilis (A) (Müll.)
Physa fontinalis (A) (Lin.)
Valvata piscinalis (A) (Müll.)
Limnea peregra (A) (Müll.)
Planorbis contortus (A) (Lin.)
Planorbis albus (A) (Lin.)

Lamellibranchiata.

Pisidium sp. (A) (C. Pfeiffer)
Sphaerium sp. (A) (Scolopli)

POLYZOA.

Fredericella sultana (A) (Bl. Mb.)

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[1] Owing to the uncertainties of specific differences in larval Trichoptera, the species given above should be regarded as types of larva found, rather than definite species that can be connected with an adult.

DENSITY OF POPULATION AND STERILITY OF THE FEMALES IN THE COCCID *LEPIDOSAPHES ULMI* L.

By EUGEN SMIRNOV and W. POLEJAEFF.
(*Zoological Institute, Moscow University.*)

(*With six Figures in the Text.*)

The density of population of both animals and plants is an ecological factor of great importance, constantly attracting the attention of investigators. In the domain of experimental work on the influence of this factor on vital functions many important data have been obtained, especially by Pearl and his collaborators. Nevertheless, a number of questions still remain open, in particular concerning conditions in the field.

Our investigations into the density of population of the Coccid *Lepidosaphes ulmi* L. were carried out in natural conditions. We came across this Coccid while studying the insect pests of the Moscow parks and squares. *L. ulmi*, together with another Coccid, *Chionaspis salicis* L., belongs to the most troublesome pests of the municipal plantations in Moscow, occurring on different species of trees and shrubs, such as the ash, poplars, limes, apples, hawthorns, etc. However, the most infected tree is the ash. The Coccid is concentrated on the trunks and branches of young trees and on the twigs of the older ones. From time to time the trees are found entirely covered by a thick layer of Coccids looking like a second bark. In cases of strong infection the trees appear badly injured: a weak growth and even a complete withering of twigs, sometimes of considerable size, are the usual results of the destructive work of *Lepidosaphes ulmi*. The Coccid has one generation every year in Moscow, and hibernation takes place at the egg stage. According to our observations in 1932, the hatching of young Coccids begins at the end of May, the egg laying being finished in September. Since the general biology of *L. ulmi* is well known, we refrain from an account of it (see, for instance, the interesting paper of Griswold (**1**)).

I.

The density of population of this Coccid varies extraordinarily. Side by side with dense accumulations, where the insects form two to three layers and overlap one another, isolated and widely disseminated scale insects can also be observed. Very different degrees of population density can often be found at the same time on a single twig. The central mass of scale insects becomes less dense outwards and little by little goes down to nothing. We have here a kind of "natural experiment": the influence of population density upon the

different properties of the scale insect can be easily studied. Bearing in mind the literature hitherto recorded, we hoped to discover if there was any connection between the density of Coccids and the egg production of their females. Our observations were made during the winter period of 1931–2, and were founded upon the females dead after the close of the egg laying. The determination of the egg production of a female does not present any difficulty, the eggs being firmly protected by her own scale and therefore perfectly isolated. In this way the egg production of each female can be exactly expressed by a number.

All the subsequent numerical data were obtained by means of the method of sample squares. A piece of bark of a definite size, 2 sq. cm., was cut out every time and the quantity of insects calculated. Thus the density of population was determined. Some further explanations of the methods used must be given here.

1. To establish the presupposed connection between the egg production (fecundity) and the density of population a single twig was used in every case. We wished to keep all factors of equal value, density excepted; but, bearing in mind the different nutritiousness of trees and local microclimatic peculiarities, the identity of this connection in various cases may be questioned.

2. The presence of males must be taken into account. According to the observations of the majority of authors who have studied this Coccid, the males occur very rarely or are altogether lacking. However, they are not uncommon in Moscow, though less than the females in number. In choosing the sample squares we endeavoured to avoid the males. Unfortunately, this has not been altogether possible in cases of dense population. In determining the value of density the males were considered equivalent to the females. As a matter of fact, owing to their smaller size, the males do not count as equivalent competitors. Nevertheless, we did not introduce any correction in the form of a special coefficient, since an insignificant admixture of males was hardly of any importance for the general results obtained, and if it was considerable, the corresponding squares were left out.

3. Among the females of *L. ulmi* half-destroyed specimens were sometimes to be found, this Coccid being attacked by the lady-bird beetle *Chilocorus* and the predaceous mite *Hemisarcoptes malus* (Shimer) (on these parasites see, for instance, Tothill (8)). Destruction of this kind makes it difficult to establish the real number of eggs produced by the female. Therefore these females were excluded from the calculation of fecundity, though taken into account in determining density.

4. It will be noticed that the Coccid population is to a considerable extent composed of sterile females, their fecundity being naturally taken as equal to zero.

5. The fecundity was rated as an average egg production, calculated for each square separately. If the number of females suitable for egg calculation

was not above thirty, the eggs were counted in all the specimens, otherwise a sample at random of about thirty females was studied. For counting, an edge of the scale used to be carefully raised, care being taken not to confuse the eggs of different females—a mistake quite possible to make with a dense population and close contact between the scales.

II.

The rate of egg production as influenced by different degrees of density of population was studied on some ash twigs, densely populated by Coccids. Table I (columns 1–4) shows the results obtained for the twig A.

Table I.

1	2	3	4	5	6	7	8	9
No. of square	Density per 2 square cm.	Females studied	Egg production per female	Egg production without sterile females	Fertile females	Sterile females	Males	Percentage of sterile females
1	13	9	37·88	37·88	13	0	0	0·00
2	23	22	46·09	46·09	23	0	0	0·00
3	41	30	46·50	49·82	37	2	2	5·13
4	41	33	46·33	50·97	38	3	0	7·32
5	42	27	39·59	44·54	39	3	0	7·14
6	45	37	46·84	49·51	42	2	1	4·55
7	65	29	45·52	48·89	63	2	0	3·08
8	95	30	31·97	39·96	81	12	2	12·90
9	98	30	29·53	31·64	85	13	0	13·27
10	124	27	29·78	38·29	106	15	3	12·49
11	125	30	37·37	40·04	107	13	5	10·83
12	130	25	21·76	32·00	105	21	4	16·67
13	137	36	39·50	49·03	124	11	2	8·15
14	149	30	22·43	33·65	110	39	0	26·17
15	209	29	38·69	48·78	161	46	2	22·22
16	220	31	43·42	56·08	172	41	7	19·25
17	237	31	43·77	54·28	164	39	34	19·21
18	378	35	29·37	44·70	202	138	38	40·59

The density of population varies in a high degree, from 13 to 378 individuals per square, the maximum being 29 times more than the minimum. The range of variability of the mean egg production amounts to 25·08 eggs, the averages varying from 21·76 to 46·84 eggs. The numerical data show that the fecundity decreases with the increase of density, this interrelation, however, not being sharply expressed. Also the maximal value of density does not coincide with the minimal egg production. A high value of fecundity (43·77) corresponds to a very dense population of 237 Coccids per 2 sq. cm., and a rather low one—37·88—is obtained for the most scanty population of 13 individuals.

Nevertheless, a negative correlation of both variables cannot be denied. Fig. 1 demonstrates this correlation in graphical form. It can be seen that the curve of mean egg production is of a characteristic form, going rapidly down at first, and then more slowly at higher densities.

As regards the fecundity of a single female, a range of variation from 1 to 108 eggs was observed. (Strictly speaking, the minimal value is zero, in so far as sterile females can occur.) Leaving aside the present twig A, the maximal egg production of a female in general attains 132.

In examining the reproduction of *Lepidosaphes ulmi* later on, we came across a quite unexpected phenomenon. It became evident that a decrease of fecundity accompanying an increase of density depends only on the number of present *sterile* females. In the 5th column of Table I the values of mean egg production are given, with the sterile females left out. It can be shown

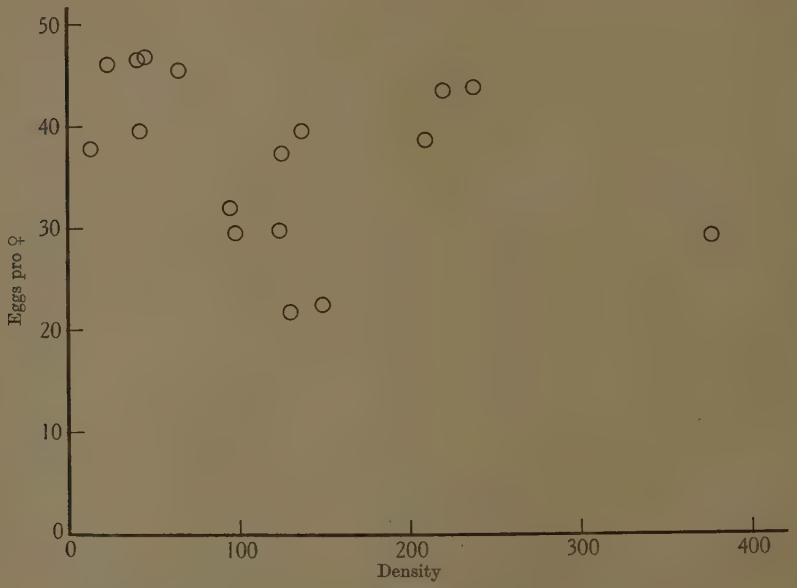

Fig. 1. Relation between density of population and mean egg production. Twig A.

that the average fecundity varies without any order when the density increases. For instance, the maximal density corresponds to a relatively high value of fecundity and *vice versa*, and no definite regularity in the connection of both the variables can be observed.

This unexpected result led us on to a more detailed study of sterility. Some ash twigs densely covered with Coccids were examined as regards the percentage of sterile females. In the right-hand half of Table I (columns 6–9) the necessary numerical data for twig A are recorded. For each square the numbers of fertile and sterile females and of males are given. The sum total of these three numbers expresses the density of population, and the relation of sterile females to the total number of females—the percentage sterility.

The comparison of these relations with the values of density shows clearly that both the variables are correlated positively and in a high degree. The percentage of sterility ranges from 0 to 40·59, this last value being especially significant. As shown in Table I and Fig. 2, the percentage of sterility increases rapidly when the density of population rises, the circles on the graph being approximately rectilinear in arrangement. The last circumstance must, however, be considered as an accidental one, for an analysis of population of other twigs shows that a direct proportionality is not the rule here.

Let us give now three further examples, each of them belonging to a single twig.

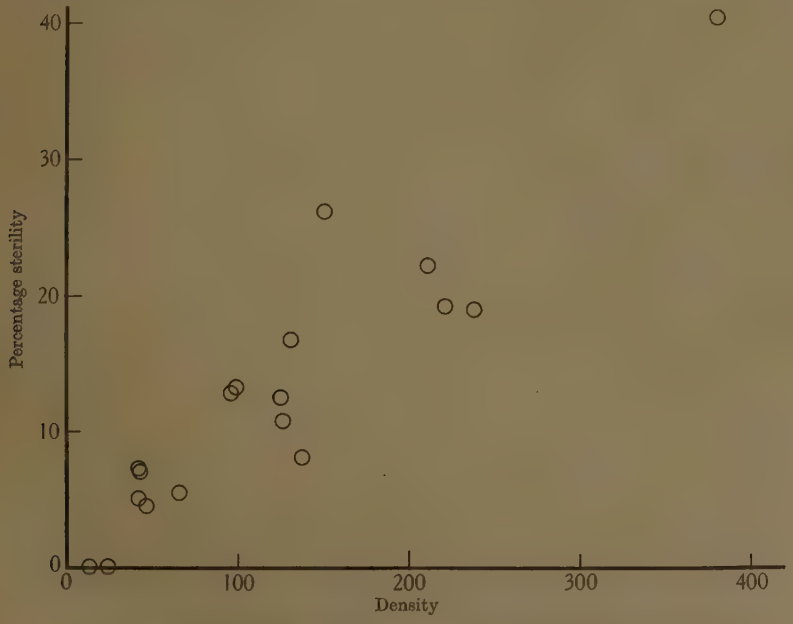

Fig. 2. Relation between density of population and sterility of females. Twig A.

Table II.

No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females	No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females
1	2	2	0	0	0·00	12	174	128	14	32	9·86
2	8	8	0	0	0·00	13	182	162	12	8	6·90
3	14	14	0	0	0·00	14	184	143	8	33	5·30
4	21	21	0	0	0·00	15	186	149	21	16	12·35
5	68	66	1	1	1·49	16	202	166	12	24	6·74
6	93	84	3	6	3·45	17	217	163	24	30	12·83
7	111	102	5	4	4·67	18	225	155	32	38	17·11
8	125	113	8	4	6·61	19	289	209	65	15	23·72
9	151	125	11	15	8·09	20	294	212	25	57	10·55
10	158	142	12	4	7·79	21	295	207	25	63	10·78
11	159	134	10	15	6·94						

A study of population of twig B (Table III and Fig. 3) confirms our conclusions as to a positive connection of both variables. In conditions of low density—from 2 to 21 individuals per 2 sq. cm.—there are no sterile females at all. The maximal value of sterility (23·72 per cent.) corresponds to one of the highest densities (289). A comparison of the results obtained for twigs A and B shows, however, that in the second case the percentage of sterility is in general lower than in the first one. (An inverse relation will be noticed as regards the relative quantity of males, which in the second case are more frequent.)

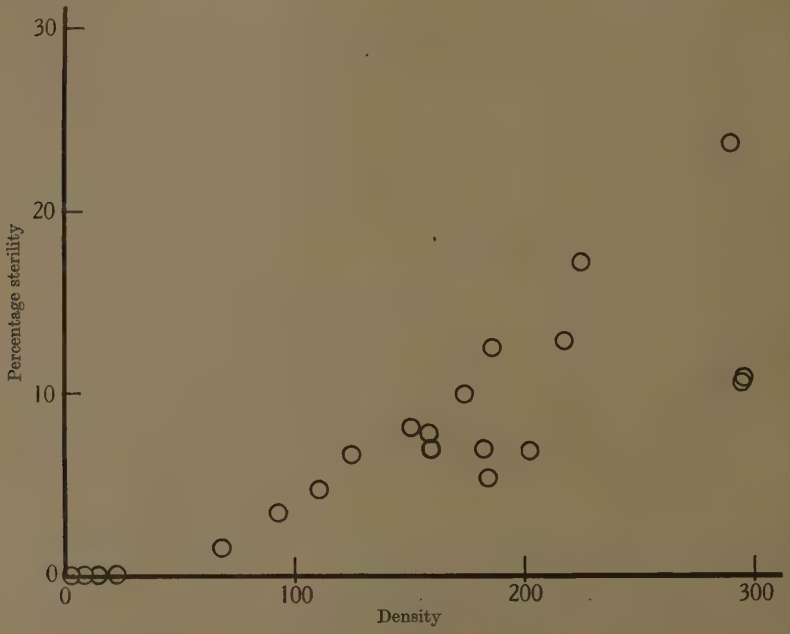

Fig. 3. Relation between density of population and sterility of females. Twig B.

In stating a similar high degree of connection of both variables in the population concerned, the peculiarities in the form of the connection must be recognised: a logistic curve being probably the best expression in this case. A logistic arrangement of dots (Fig. 3) is perhaps more especially shown at low and moderate densities. On the other hand, a slowing down of curve growth at high densities cannot be denied.

The next example (twig C, Table III and Fig. 4) resembles A as to the value of sterility. It is true that the extreme values of sterility appear to be lacking in the present population, this fact being evidently due to the absence of high densities, the highest being only 234. As to the form of the connection,

an exponential curve seems to be preferable. Bearing in mind the absence of higher densities, the presence of a lower part of the S-shaped curve might be assumed here.

Table III.

No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females	No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females
1	64	54	1	9	1·82	9	152	135	2	15	1·46
2	69	57	3	9	5·00	10	159	142	16	1	10·13
3	70	57	1	12	1·72	11	159	140	18	1	11·39
4	95	84	2	9	2·33	12	161	125	28	8	18·30
5	101	100	0	1	0·00	13	192	165	26	1	13·61
6	112	95	8	9	7·77	14	208	162	27	19	14·29
7	113	101	9	3	8·18	15	234	137	47	50	25·54
8	123	87	9	27	9·37						

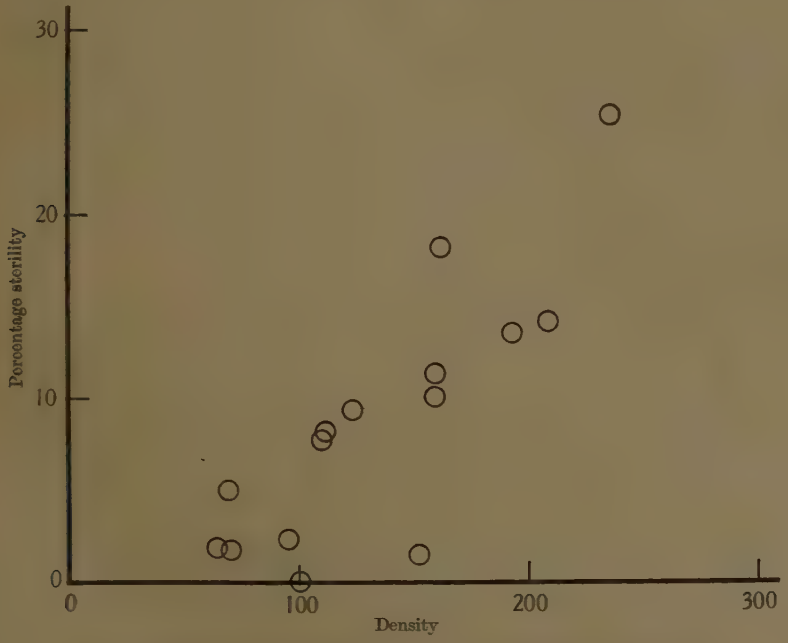

Fig. 4. Relation between density of population and sterility of females. Twig C.

In the last example (twig D, Table IV and Fig. 5), we have abundant data, though belonging to low or moderate densities. The percentage of sterile females must be evaluated as comparatively high, attaining its maximal value (14·42) at the density of 113. It can be shown from Fig. 5 that there is a considerable dispersion of dots. The character of the curve in question cannot be determined with certainty. In order to facilitate the study of the rule regulating the disposition of the dots, we calculated the mean values of

sterility according to the classes of density, these values on the graph being marked by black circles. In any case an increase in the number of sterile females at high densities is indubitable. This relation is evident in all the four examples.

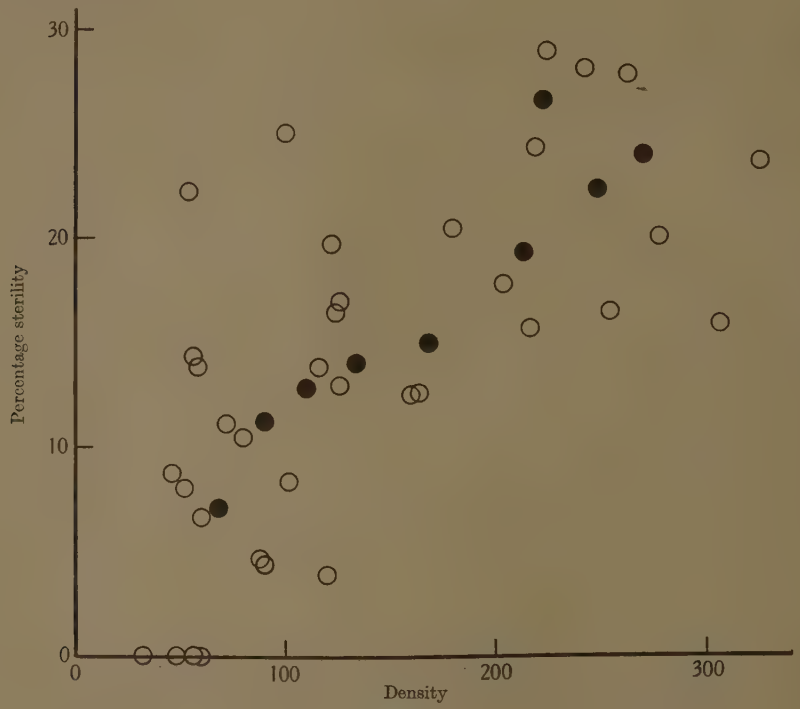

Fig. 5. Relation between density of population and sterility of females. Twig D.

Table IV.

No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females	No. of square	Density per 2 sq. cm.	Fertile females	Sterile females	Males	Percentage of sterile females
1	16	16	0	0	0·00	19	61	55	6	0	9·84
2	23	22	1	0	4·35	20	62	56	5	1	8·20
3	24	23	0	1	0·00	21	63	58	4	1	6·45
4	26	24	1	1	4·00	22	63	54	5	4	8·47
5	27	24	3	0	11·11	23	80	75	5	0	6·25
6	28	28	0	0	0·00	24	82	74	5	3	6·33
7	28	26	2	0	7·14	25	90	79	9	2	10·23
8	29	27	2	0	6·90	26	102	92	9	1	8·91
9	30	30	0	0	0·00	27	108	94	8	6	7·84
10	30	29	1	0	3·30	28	110	94	13	3	12·15
11	36	34	2	0	5·56	29	113	89	15	9	14·42
12	40	36	2	2	5·26	30	122	104	17	1	14·05
13	44	42	1	1	2·33	31	127	100	9	18	8·26
14	45	44	1	0	2·22	32	132	112	18	2	13·85
15	50	42	6	2	12·50	33	139	108	12	19	10·00
16	51	46	2	3	4·17	34	153	139	12	2	7·95
17	58	54	4	0	6·90	35	163	135	18	10	11·76
18	60	55	1	4	1·96						

III.

As pointed out above, a diminished egg production of *Lepidosaphes ulmi* at high densities of population cannot be explained by the reduction of the egg number produced by single females, an increase in the number of sterile females being the real cause. The question arises as to the factors producing sterility.

Among published studies on the effect of density of population upon the egg production of animals, the results Pearl (**3**, **4**, **5**, **6**) and his collaborators obtained from their experiments on the fruit-fly *Drosophila* are of particular interest to us. In their earlier papers (1925–7) the authors strictly speaking have had to do with fertility (number of adult progeny produced), the last paper of Pearl recently published (1932) being given to the study of fecundity (number of eggs produced) as influenced by different densities of population. The reduction in mean fecundity of *Drosophila* at high densities, as proved by the experiments of Pearl, agrees with our own observations on *Lepidosaphes ulmi*; but his results have nothing to do with the phenomenon of sterility in the females. In as far as the egg laying of single females has been traced, the same individual *Drosophila* exposed to conditions of high density used to diminish its rate of egg production as compared with the egg laying at low densities.

According to Pearl, the crowding of flies in a limited space produces a depression of the vital functions, among them egg laying. The flies disturb one another while resting, feeding, etc., and this disturbance causes an increased expense of energy.

The question arises, whether the interpretation of Pearl can be admitted for the occurrence of sterility in *Lepidosaphes ulmi*. To obtain an answer we need to know more about the conditions accompanying sterility. It must be noted first of all that two kinds of sterile females can be observed. The females of the first class are not much smaller in the size of their scales and bodies than the fertile females producing eggs normally. Another state of affairs is found after the death of the females. The body of a dead fertile female shrinks and becomes shrivelled, while that of a sterile one is hardly reduced in size, though being completely flattened. In the end the latter appears much larger than the former and can be easily distinguished. Fig. 6, *a* and *b*, shows the scales and bodies of fertile females drawn from below, the bodies being left in their natural position as regards scales. In Fig. 6 *c* a sterile female of the first class is seen, its larger body being easily noticeable.

The second class of sterile females is characterised by a small and short scale, hardly above the size of the body, which itself is very small (Fig. 6 *d*). According to their dimensions these females are similar to the larvae of the second instar, but a morphological analysis obliges us to look upon them as imaginal forms. After such a female dies its body becomes flattened without

shrivelling or shrinking, analogous to a sterile female of the first class. It can be shown by a comparison of the figures that the bodies of this kind are about the same size as those of shrunken dead fertile females.

As to their situation on the bark the sterile females of the first class do not differ from the fertile ones. But the position of sterile females belonging to the second category is different; these as a rule occupy the upper layers of the Coccid accumulations, and are noticeable on account of their insignificant size.

In conditions of high densities we must assume the presence of a struggle for space. Crowding takes place; the Coccids press one another, this pressure

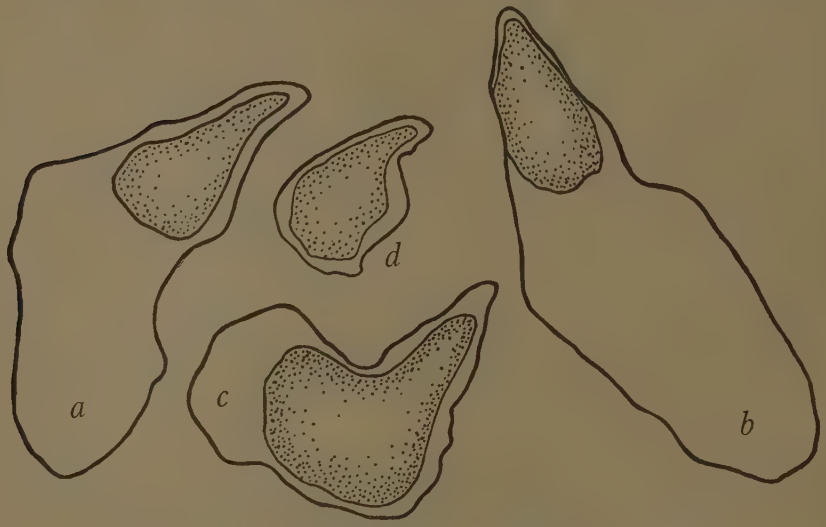

Fig. 6. Ventral view of fertile (*a*, *b*) and sterile (*c*, *d*) females; *c*, a sterile female of the first class; *d*, a sterile female of the second class.

leading to different alterations in the form of the scale, to curvatures and distortions. At the same time a struggle for food seems also to be very probable, the specimens situated above meeting with more difficulty in their feeding than those close to the bark. It is of interest that the beginning of crowding can be already seen at the first larval instar of the Coccid. After a short migration and choice of a suitable place the young larvae fix themselves on the bark strongly and permanently. It was observed many times that the larvae even at that moment overlap one another. Naturally, in proportion with the growth of the insects, especially of their scales, the crowding increases to a considerable degree, reaching a maximal one at the adult stage. In these circumstances some of the future sterile females (belonging to the first class) are nevertheless able to grow to the normal size,

but are unable to begin egg laying, for these females, if dissected, show the presence of eggs. On the other hand there are females (the future steriles of the second class), which are subjected to the action of still worse conditions. They can hardly metamorphose into adults (as shown by their smallness), being even incapable of developing eggs. The latter has been proved by means of dissection.

In this way it may be on the whole accepted that a struggle for space and food is the probable cause of sterility under conditions of dense population. There is no contradiction between this conception and the cases which have sometimes been observed, when the ash twigs were entirely covered by sterile females (of the second class). It may be supposed that not a high density of population but a drying up of the twigs led to a premature dying off of the Coccids in these instances. We should be quite satisfied with this explanation but for the existence of an incomprehensible circumstance. What is the reason why unfavourable external conditions, though they are able to produce an absolute sterility, do not influence the mean number of eggs laid by fertile females at high densities? It is true that females can be found producing insignificant numbers of eggs. At low densities the sterile females being infrequent, they could be evaluated without any difficulty as extreme variants of a normal frequency curve. At high densities, however, their number rises to such a degree that the sterile females create a special mode, the curve becoming bimodal (the first mode corresponding consequently to the average value of the egg production). For the present we have no idea of the possible factors producing this bimodality. It is to be hoped that in future specially arranged laboratory experiments will throw some light upon this problem.

According to the observations of Lignières (**2**) the predaceous mite *Hemisarcoptes coccisugus* Lign. (=*H. malus* Sh.) sucking out the Coccids causes a strong reduction of the egg quantity to be produced by the female. The phenomenon of female sterility is attributed by Reh (**7**) to the same agent. If so, the disproportionate increase of the number of sterile females that we have observed under conditions of overpopulation must be explained by the dense accumulations of Coccids being especially attractive for mites. In this way, the high density of population would become an indirect cause of sterility. This assumption, however, can be hardly accepted in view of the facts to be communicated in a second account on *Lepidosaphes*.

SUMMARY.

It follows from what has been said above, that the density of population may be considered as a factor regulating an excessive reproduction of *Lepidosaphes ulmi*, overpopulation causing a hindering of further population growth. This circumstance must be taken into consideration in prognosticating any future outbreaks of the Coccid.

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A CONTRIBUTION TO TROPICAL AFRICAN BIRD-ECOLOGY

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(*With Plates II and III and two Figures in the Text.*)

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I. Introduction.

Although all work on bird biology contains much of ecological import and geological considerations have underlain some of the best modern systematic ornithology, explicitly ecological work on African birds has been rare. The bias in favour of the geographical aspect of bird distribution has been strong; so strong that since the publication of the *Systema Avium Aethiopicarum* African bird geography in its old sense may be said to be within sight of completion, while on the other hand the definition of the range of each form in terms of environmental factors, omitting so far as possible local incidentals, has hardly begun.

Clearly the ecology of any given bird can only be worked out on the basis of critical local studies carried out on comparable lines. Such studies would lead to substantial advance in African ornithology. The optimum and the limiting conditions for each form would ultimately be determinable. Climographs of distribution could be prepared and the factor of prime significance in determining the range of each form might emerge. The sub-species that were merely in geographical isolation would be distinguished from those grounded in ecological adaptation, and between the latter the significant differences could be stated. The existence of "physiological races" would become apparent, forms like those demonstrated in other classes of organisms, morphologically indistinguishable but of specialised ecology.

The present paper has arisen out of an attempt to make a detailed bird survey of a particular area, the Usambara Mountains of Tanganyika Territory,

as a contribution to the scheme of research suggested above. I have the advantage of being resident there, and moreover the Usambara Mountains are unusually well adapted to provide the essential facts, unobscured by accidents of topography, of the ranges of many forms. The area presents a large variety of habitats in the separation of which geographical distribution plays the smallest possible part; and it is almost unique in Africa in exhibiting a series of evergreen forests, which provide a homogeneous complex of niches, from sea-level to 7500 ft. practically without interruption. (A map of Usambara showing the forests appeared in the *Ibis* for 1932, facing p. 492.) Also the correlation of climate with altitude is markedly different in Usambara from that in other African mountain areas. Data from such an anomalous region must be of special value when a comparative study is made of distribution in several areas, as tending to isolate the influence of particular factors.

In seeking to collect data on the significant variables of the environment I have been faced at the outset with the difficulty of deciding upon what variables attention should be focussed. Such an area as Usambara, close to the Equator, and mainly evergreen, presents problems strange to the ecology of the temperate zone. In Usambara there are no lethal temperatures, and for the most part there is no seasonal interruption of food supply. Further, in Tropical Africa the life-zone through which at least one homogeneous complex of niches—that conditioned by evergreen forest—may persist, is 10,000 ft. high. The present paper is an attempt to take stock anew of the potentially significant variables in this unfamiliar environment, and particularly of the enigmatic "altitude" so often referred to as if it were a simple factor. The following pages will inevitably include much that is commonplace to experienced ecologists; but as critical methods have not been applied extensively in African ornithology, certain fundamentals require to be restated. Attention will also be drawn to the subject of bird eco-climates; for the extent to which the temperatures actually experienced by birds differ from those recorded by ordinary meteorological stations has not been generally appreciated.

Various opinions have been given on the factor of most importance in determining bird distribution in Africa. Chapin (1923) thus summarised his main thesis, in which he had the immense low-lying West African region particularly in mind: "It is through these different types of vegetation (steppe, savannah, forest) that the rainfall determines the distribution of birds." For, in his experience "avifaunal lines are never more sharply defined than the changes of composition and habit of the vegetation." He considers that "although temperature may be a distributional factor of weight it acts most visibly along certain critical lines, as, for instance, where occasional frosts occur....Other similar lines are found on mountains, where trees disappear." In a later work Chapin is inclined to attribute "no marked influence" to "temperature alone" in the Congo "until an elevation of 5000 ft. is reached"

(1932, p. 81). Bowen (1932) has divided the African avifauna on a temperature basis, but he does not discuss the manner, direct or indirect, in which temperature might exert an influence on birds.

It is hoped to publish the detailed Usambara survey data elsewhere (a synecological study has been accepted for publication in the *Journal of Ecology* in 1935), and subsequently to discuss them in this *Journal*, with particular reference to the suggestions of Chapin and Bowen. Meanwhile it seems to be essential at the outset to recognise the close interdependence of the major factors in the environment. Thus in the opinion of one distinguished ecologist, "Temperature and moisture are so interrelated in controlling the geographical range of organisms that the two are often confused and it is difficult to separate out either moisture or temperature as a definite controlling factor in the geographical distribution of animals" (Chapman, 1931, p. 105). Here, then, is special need for caution in attempting to designate prime factors in African bird distribution. The temptation to over-simplify is one that has constantly to be resisted. "It is fairly useless to make elaborate 'laws of distribution' based entirely on one factor like temperature, as has often been done in the past. It is too crude" (Elton, 1927, p. 43). With this in mind, an attempt has been made to approach the whole question *de novo* in a critical spirit.

A suitably humble—if not despairing—frame of mind towards the complexity of our problems is induced by the following quotation from a recent review of insect ecology:

"An insect living under natural conditions is never exposed to one isolated climatic factor, but to the continually changing combinations of several. While in the study of the responses of an insect to environment it is necessary first to apply the analytical method, and to investigate the influence of each factor separately, it would be wrong to assume that the response of an insect to the combined action of several factors will represent merely a sum of the responses to each of the factors involved. Indeed, we must first satisfy ourselves whether this is true, or not, by studying experimentally all the more usual combinations of factors" (Uvarov, 1931, p. 80).

Recent work on plants has developed this point further. It has been shown experimentally how the nature of an organism's reaction to any one factor may be affected by variation in other factors (cf. Gregory, Crowther and Lambert, 1933).

I desire to express my general indebtedness to the scientific officers of this Research Station. They have freely given me assistance on technical points; and the diversity of their interests has aided the cultivation of a broad outlook.

II. Altitude and its concomitants.

Altitude has often been referred to as if it were a simple factor, and it has always been regarded as of great significance in determining the distribution of living things. For example, the wording of the British Museum collector's labels invites the insertion of the altitude at which the specimen was taken, although it does not require any other particulars of the bird's associations. This conception of the importance of "altitude" may be correct, but there appears to be no general agreement, and, indeed, surprisingly little discussion, as to the nature of the influence of altitude on the organism. Thus Chapin (1923) remarks that "the striking difference [in avifauna] between the Tsavo desert district and the highland veldt to the westward has sometimes been spoken of as due to altitude. This is probably only involved so far as it affects rainfall," and hence, by inference from the main thesis of the paper, vegetation. Chapman, however, in his Andean work (1926) appears constantly to imply the potency of some factor linked with altitude, other than vegetation. I have failed to find any explicit statement of his views, but such passages as this (page 128) appear to indicate his belief in the direct influence of temperature as the critical concomitant of altitude: "From these colder regions [of southern South America] the Condor, no less than diminutive Sparrows, have extended their range toward the Equator, increasing their altitude with decreasing latitude and thereby remaining in a life-zone similar to that from which they started." In any case it appears that there is room for a critical examination of the whole question of the influence of altitude.

I may say here that I came to the Usambaras without any preconceptions whatever on this subject. I had never lived or worked in a mountainous country. But as I began to learn something of the distribution of the local fauna I was astonished to find that altitude above sea-level had the appearance of ruling the distribution of many species. It was as if every bird carried a pocket aneroid. As one travelled about the mountains the same species were to be expected at the same heights above the sea. One striking example may be cited at this stage. When I went to the West Usambara plateau, which is all above 4000 ft., I met for the first time a number of species not seen in several years' residence and intensive collecting at 3000 ft. on the East Usambara plateau (Amani). In the East Usambaras there is one ridge, at the north end, that rises appreciably above 4000 ft. The total area above that height is about 3 sq. miles. This was searched for West Usambara species, with the result that a single day's collecting produced three still not encountered at 3000 ft. There are no obvious biotic factors to account for this limitation of range. The impression conveyed is that altitude *per se* is of significance. But obviously altitude can only make itself apparent to the organism through one or more of its physical concomitants, i.e. environmental factors. These factors

will be discussed severally; meanwhile, the degree of their connection with altitude must be glanced at.

Chapin's tacit assumption when he compares the Tsavo area and the Kenya Highlands, that increased altitude means increased rainfall, is one that can be supported by many local examples. There is certainly a tendency for precipitation to be greater at higher elevations, but this is not in consequence of any general principle. It is the result of local topographical factors. Thus, the Taru Desert, which Chapin had in mind in the remark quoted, at an altitude of about 1000 ft. above sea-level, gets 25 in. of rain a year. A hundred miles to the south and the same distance inland the rainfall at 800 ft. is 70 in. (at Tongwe Mission in Usambara). Elsewhere in Usambara, Amani at 3000 ft. has a rainfall of nearly 80 in., Shume at 6400 ft. one of under 30 in.

Factors that are of more importance than the actual amount of annual precipitation in governing the type of vegetation are the distribution of the rainfall and the temperature. In a cooler climate evaporation is lower. So far as vegetation is concerned the same amount of rain "goes further." Köppen in making his classification of the climates of the world (1918) gave special weight to this modifying factor. Following him McDougall has drawn up a chart (1925) showing the effect of the interaction of rainfall and temperature. Thus, it is shown that if the mean annual temperature is 60° F. (15° C.) 80 in. of rain are required to produce equally humid conditions as result at 40° F. (5° C.) from 50 in. The absolute saturation deficit of the air is probably the criterion that should be applied in determining the rainfall efficiency, but African data for this calculation are so scanty and unsatisfactory that it cannot be used at present.

Decreasing temperature is certainly an immediate and predictable effect of increasing altitude—at the rate of about 2° C. per 1000 ft. as a world-wide average. But temperature is by no means always correlated with altitude to the same degree, nor, of course, with latitude. Thus, in the Usambaras the temperatures run much lower than the altitude and latitude would lead one to expect. At Amani (3000 ft.) the mean temperature is that of Kenya and Uganda[1] at about 5000 ft., and of stations at 3000 ft. in the Shire Highlands of Nyasaland, which are 10° further from the Equator. Text-fig. 1 shows comparatively the temperature-altitude correlation in several African areas. Data for Kenya and Usambara have been in part supplied by the B.E.A. Meteorological Service and in part derived from successive years of the "Mitteilungen aus den Deutschen Schützgebieten." Data for other areas have been derived from Knox (1911); Murray (1922) for Nyasaland; Sayers (1930) and *Der Pflanzer*, vol. 8, 1912, Anhang, for Kilimanjaro; Meteorological Maps, Survey of Egypt, Cairo (1922), for the neighbourhood of Ruwenzori. It is,

[1] Cf. the *Ruwenzori Report* (Ogilvie-Grant, 1910, p. 369), where reference is made to "hot tropical valleys" at 6000 ft. There is nothing of the kind at 6000 ft. in the Usambaras, or even so low as 4000 ft.

moreover, worthy of remark that the respective elements making up the mean temperature do not decrease to an equal degree with increasing altitude. Although the data to hand are only those for the Usambara and for Kenya this is doubtless a general phenomenon. The physical basis is presumably increased outward radiation at night owing to the thinner atmosphere at high altitudes. The annual means (mean maxima and mean minima for Kenya as published by the British East Africa Meteorological Service) for various altitude zones are shown graphically in Text-fig. 2. It is evident (i) that the minimum decreases almost exactly twice as fast as the maximum, and 1½ times as fast as the mean; (ii) that the higher the altitude the more extreme the climate (compare Samoa, where the mean daily range at sea-level is 6·4° C., at 2000 ft. 9·6° C. (Buxton, 1930)).

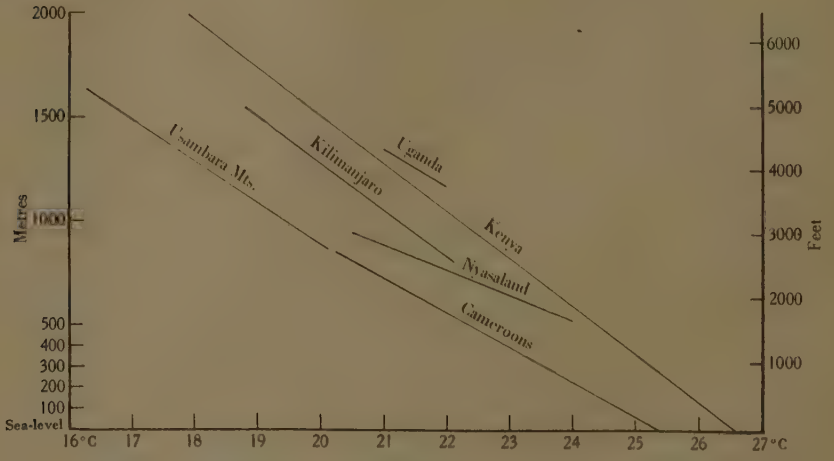

Fig. 1. Gradients of annual mean temperature × altitude in Tropical Africa.

On the whole, it is clear that if we are trying to ascertain the limits of a species' temperature tolerance, its altitudinal limits are by themselves far from giving an accurate indication. Moreover, cutting across the general climatic variations and modifying them to a surprising extent are the localised modifications of climate, especially the eco-climates engendered by vegetation. These are discussed in a later section.

There is still another precaution that must be observed by the ecologist in stating, or accepting a statement of, a species' vertical range. Where the bird's connection with a certain botanical formation is close, we shall often find that its lower and upper limits are those of the formation. This particularly applies to birds of tall evergreen forest. By a historical accident, organised man's first appearance in Tropical Africa armed with fire and with iron tools

has coincided with an epoch of general desiccation. The result is that evergreen forest, already of less extent than under a more humid climate, has been restricted more and more to the mountain-tops. In fact, at the present day there is but little evergreen forest left below 5000 ft. in the eastern half of the continent. Consequently, in East Tropical Africa a forest bird tends to be looked upon as a mountain bird. This is often true in essence as well as in appearance; but we must constantly be on our guard against accepting as a species' natural bounds what are in truth artificial restrictions of recent date.

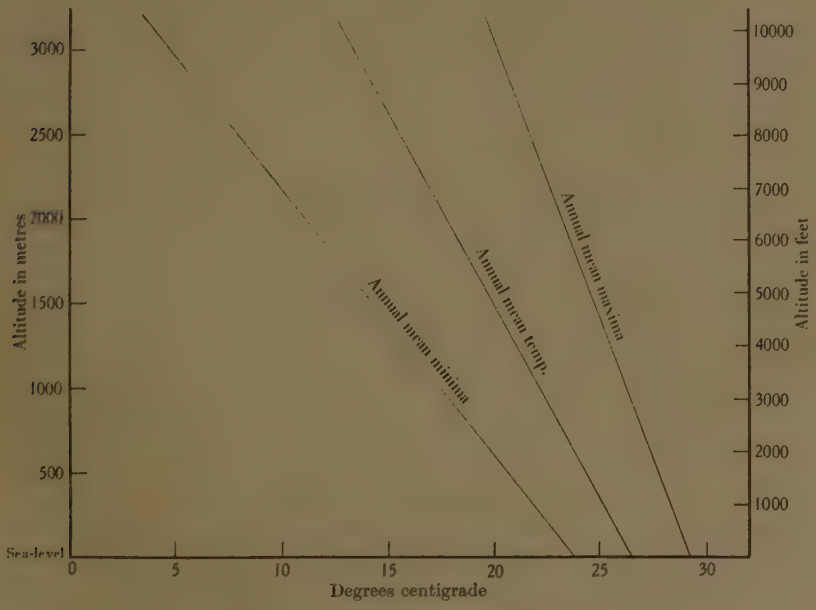

Fig. 2. The increasing extremes of climate with altitude (Kenya).

This prepossession may in part account for the astonishing and misleading list given by Bowen (1932, p. 269) of "species characteristic of the savannas and drier belts," Category C, "Confined to the East Coast." Practically half the twenty-one species cited are characteristic of closed forest or restricted to the extreme coastal strip, which is comparatively humid.

In conclusion it may be said that from the point of view of the ecologist, an altitude expressed in feet or metres is best regarded as nothing more than a convenient shorthand method of indicating a complex of meteorological conditions and biological associations, which invariably require to be defined for the particular district concerned.

III. The factors potentially significant in bird distribution.

These may conveniently be considered under three headings: (1) Biotic, (2) Climatic, (3) Subjective factors.

(1) *Biotic factors.*

At the outset a distinction requires to be drawn between directly and indirectly operating biotic factors.

(*a*) *Direct biotic factors.*

This term covers the most obvious and concrete elements in a species' economy; the presence or absence of suitable food, nesting sites, nesting material, of enemies and of competing species. These direct biotic factors have often been held to be the determinants of bird distribution. There can, of course, be no doubt of their great importance, but they can no longer be regarded as all-sufficient.

Thus, in the case of the big hornbill, *Bycanistes cristatus*, its most obvious requirements in life are quantities of fruit and very large holes in trees to breed in. This hornbill is absent from the "Miombo Bush" that covers so much of East Africa. "Miombo Bush" contains practically no trees large enough to provide holes for the bird. Here, then, is a direct biotic factor capable of accounting for the bird's absence from the "Miombo Bush," even if all the other local factors were within its tolerance. But when we find that, given a continuous sheet of evergreen forest full of huge old trees and providing plenty of fruit throughout, these hornbills shun one part of it, we begin to seek factors other than the direct biotic factors. In Usambara dozens of species present just such a problem.

One's general ideas on the efficacy of competition between individual species as a mutually limiting factor must suffer some modification when the peculiar circumstances of the tropics, and in particular of tropical forests, are considered. We will for the sake of simplicity deal with evergreen forest conditions where all the local peculiarities are found in their most exaggerated form. First, it is clear that, except for those birds that live in holes, competition for the essentials of nesting cannot be a limiting factor. The provision of nesting sites and nesting material is so abundant in evergreen forest that competition for food would intervene as a prior limiting factor. As regards food, the two main types available in the forest are fruit and insects. In the forests I know best the supply of fruit appears to be perennially abundant, and vast quantities of it fall uneaten to the forest floor. And it has been one of the most remarked features of tropical forest ornithology that in its pursuit co-operation in the pursuit of insect food in great measure replaces competition. Swynnerton's notes (1915) on this subject in the Chirinda Forest are applicable, to a large extent even specifically, to the Usambaras, and doubtless to other African forests. In certain species it may be possible to demonstrate a fully

competitive instinct and developed territorial prepossessions; but on the very broad general grounds given above it appears that within our area competition as a direct biotic factor is not likely to be of much weight.

Moreover, the mutual exclusiveness of competing species, so that their common boundary is the resultant of the population pressure from both sides, probably has practical importance mainly in large areas of uniform environment. The area considered here is highly mountainous, with a variety of habitats packed into a small space. Each one is, on the geographical scale, of trifling extent. In such circumstances it appears that even if a boundary between any two local species is the resultant of their competition, the site of it must be determined within narrow limits by the extent of each species' optimum environment. Therefore in subsequent discussion the direct competition factor will be ignored.

(*b*) *Indirect biotic factors.*

These may be of the most varied and obscure nature. Vegetation factors are of more general, as opposed to specific, potential importance than any zoological factors that can be conceived, simply because vegetation development can change the whole physiognomy of an environment. All birds pass more or less of their lives within a couple of hundred feet of the ground. Most of them are tied almost as closely to the earth for critical periods in their lives as the average mammal. Within the narrow zone they inhabit, vegetation may take up an important part of the space. For most species of bird vegetation provides the furniture of their habitat, for many the walls and for some the roof as well. Essential features of the habitat may remain true to type either in time or space, but may change specifically. Thus in every stage of its succession a regenerating evergreen forest in Tropical Africa will provide a variety of dense bush cover and berries. But the bushes and berries present at the beginning and at the end of the process will not be the same, nor will the attendant insect population. Again, a typical mountain forest of Tropical Africa provides the same set of habitats and niches as does an evergreen lowland forest, but the species of plants providing the furniture and framework of each are different in the two forests. In such a case essential material requirements may be present continuously for any given bird in general type but with specific changes. If then, as usually happens, the range of the bird is less extensive than that of the type of its material needs, the hypothesis of a direct biotic (vegetational) factor may be held to break down, but that of an indirect (vegetational) factor operating through subjective factors may be tenable.

Especially when vegetation bulks large in the absolute sense, modified climatic conditions tend to be produced within its immediate influence. We know next to nothing about the eco-climates associated with various vegetation types in the tropics: they are only now beginning to be studied. As in

temperate regions, there must however be well-marked divergencies, specific to at least the main botanical formations, from what is commonly regarded as the "general" local climate, i.e. the climate as usually measured in a screen 3 or 4 ft. above the ground. It is at first sight to be expected that these eco-climatic differences will *per se* be of less importance to birds than to insects and plants: but when it is realised that eco-climates conditioned by vegetation and existing side by side in an area even so small as a few square yards, may differ as much as the "general" climates of altitudes separated by thousands of feet or of countries a thousand miles apart, it becomes obvious that this effect of vegetation is an indirect biotic factor to be borne in mind even if we lack the data to assess it in numerical terms. Reference is made in Section IV to certain eco-climates important in Tropical Africa.

Before leaving the subject of indirect biotic factors of potential general importance, a possible zoological factor may be cited in the presence or absence of a vector of a parasitic disease. Mosquitoes and malaria are obvious examples in point. The mosquito population tends to fall off rapidly with increasing altitude and to change in specific composition. It is conceivable that the presence of certain mosquitoes at low altitudes might set an effective limit to the high-altitude avifauna, which had never acquired immunity to bird malaria. However, it is a fact that at present nothing is known of the incidence of bird malaria in Africa (Mr J. W. McHardy, Medical Entomologist to the Tanganyika Governments, *in litt.*), although it has received much attention in America. The parasites are specifically different from those concerned in human malaria (Wenyon, 1926). Filaria is another parasite in point (cf. Webb, 1931).

(2) *Climatic factors.*

Next to nothing accurate seems to be known of the direct significance of any of these factors to birds, and particularly to wild birds. Direct effects only are considered under this head. Indirect effects can of course be regarded as existing, but their operation is through biotic factors. Experimental data will always be difficult to obtain, for the living material with which we are concerned is perhaps the least susceptible to laboratory treatment of any class of organism. In this respect the botanist and the entomologist are to be envied. At least a beginning has been made in knowledge of insect responses to climatic factors. Chapman (1931) summarised a mass of data on the reaction of animals to various factors, but making all allowances for the fact that he wrote "with especial reference to insects," his citations dealing with vertebrates are suggestively scanty, and are few indeed for birds. For insects alone Uvarov (1931) also has provided a critical and thoroughly up-to-date summary.

Such progress as the entomologists have made is of interest to us as a guide to what factors are likely to be of significance to animals in general and

in what way. But several cardinal differences between insects and birds must be borne in mind. Unlike insects, birds are warm-blooded animals. The temperature range within which an insect is capable of activity may be less than 25° C. and beyond the extremes of its active range it may fall into complete inertia within 2° C. (cf. Chapman and others, 1927). Moreover, birds are extremely mobile except for the comparatively short initial helpless stage of their lives; and during that stage they are for the most part enveloped in special conditions maintained by the parent. The differences between insects and birds are too great for any close reasoning from analogy to be permissible.

Under climatic factors, humidity, light, wind, pressure and temperature have to be considered. The first three can be disposed of briefly at the start: the subject of eco-climates, which is of most interest to us on the temperature side, is discussed in section IV.

(*a*) *Humidity.*

Birds in general are likely to be much less susceptible than other animals to the direct effects of humidity. For in the case of shortage of moisture birds can move comparatively long distances to drink, and moreover they are notoriously adaptable in this respect. Thus Lynes (1925) found that besides the native birds, which were habituated to desert conditions, many Palaearctic birds passed the winter in parts of Darfur where there was neither accessible surface water nor dew for months on end. In case of excess of moisture birds are not likely to be affected unless they are susceptible to damp-engendered diseases. These are perhaps most likely to be operative on birds just out of the egg or the nest. It is common experience that a "cold wet spring" is bad for poultry rearing, and there the conditions are such that there is no question of the food supply being affected by unfavourable weather.

There is the possibility that some birds, like most human beings, may experience discomfort when the saturation deficit of the air is very low—"raw cold" and "muggy heat"—and may shun areas where this uncomfortable condition prevails. But this question of the potential significance of humidity through the comfort impressions of the subject is a particularly difficult one because the idea of relative humidity is inseparably bound up with temperature. The investigations quoted by Chapman (1931, p. 111) show that an unexpectedly wide range of relative humidity can convey to the human subject a similar impression of comfortable conditions if the temperature is suitably adjusted. But we have to face the fact that birds may be influenced by humidity in their impressions of comfort and discomfort quite differently from human beings, and that avian species must differ in this respect widely between themselves.

It is indeed only too clear that we have not the remotest idea to what extent humidity may operate directly to determine birds' ranges, if at all: but we shall probably be safe in concluding that except in a few extreme

cases (e.g. sandgrouse, *Pterocles*) any direct influence of humidity is small in comparison with the immense importance of humidity in determining the botanical elements in the habitat. The tendency for plumage colours to be darker and richer in more humid areas is well known—the so-called Gloger's law. How far this is the direct effect of humidity and how far of other factors, especially light, is doubtful and probably variable from species to species. For example, with the crested larks (*Galerida cristata* subspp.) of the Near East there is reason to suppose that humidity does not account for their conspicuous colour gradations (cf. Meinertzhagen, 1921, p. 642). On the other hand I believe that an American worker (? Beebe) succeeded experimentally in producing darker plumage in a dove by manipulating the humidity of the laboratory environment, but I cannot quote the reference.

(*b*) *Light.*

Although it may be of comparatively little importance to birds in many regions of the earth, light is of special interest to us because of the dominance of evergreen forest in our area, with a whole fauna confined within the shade of its canopy. Sun-flecks reach the ground, but between them the average light intensity is of the order of one-thousandth of that of the open air. In our experience individual birds of the species inhabiting the interior of the forests do not seek, and appear to shun, flecks of sunlight. It is then conceivable that a bird living near the ground in the forest may be physically incapable of supporting the impact of full sunlight even if the material necessities of life are available. The question of the optimum composition of the light can at this stage only be left untouched. The light that reaches the forest-floor between the sun-flecks is certainly very different from the white light of the open air: and recent work has shown a possibility that light of different wave-lengths may have different effects on testis activity (cf. Bissonnette and Wadlund, 1931).

Furthermore the amount of ultra-violet radiation penetrating to the lowest stratum of the forest appears to be extremely small, probably even less in proportion than the visible light. The importance of ultra-violet radiation in elaborating vitamin D from the ergosterol in the preen gland has been recently demonstrated in certain northern species of birds (Rowan, 1931, pp. 57 et seq.). It appears possible therefore that birds confining themselves to the deeply shadowed interior of the evergreen forest may be specialised in this respect.

High (visible) light intensity and high temperature tend to go together, and their effects will tend to be confused.

(*c*) *Wind.*

Except perhaps in peculiar regions of the earth where high winds are a very constant and pronounced phenomenon their mechanical effect is likely to be of much less importance to birds than to plants and insects, although birds certainly seek cover and sheltered hollows in windy weather. In our

area wind can hardly be of any significance. It is, however, a fact that the stillness of the air is one of the characteristics of the forest eco-climate. Birds of the undergrowth are never during the whole of their lives exposed to anything stronger than a draught; and even in the canopy the force of any wind is mitigated.

(*d*) *Pressure.*

With species that in our area appear to be limited in distribution by some factor cutting across an approximately homogeneous habitat, it is natural that barometric pressure should present itself as possibly significant. We shall clear the ground if we can dispose of its pretensions.

In the first place, barometric pressure is the factor that varies most directly with altitude. It decreases with increasing altitude: and the same altitude implies the same pressure irrespective of locality and latitude. In the tropics the daily variation in barometric pressure tends to be greater, and the seasonal less, than in the temperate zones. Temperature also affects barometric pressure to a slight extent. These causes of variation are however small compared with those resulting from change of altitude. They are equivalent to those caused by a few score of feet in ascent or descent, whereas we are dealing with thousands of feet.

At first sight it appears to follow from this that a hypothesis of the significance of pressure in determining the distribution of a bird could be proved or disproved by demonstrating that the same morphological form did or did not occur between the same altitudes on different mountains. From my experience it appears that it would not often be possible to demonstrate such a unity of altitude choice, and there are, of course, very notable exceptions, such as the numerous species referred to by Chapman (1926) in the Andes. But the question of pressure cannot on this account be quite disposed of at this stage for two reasons. In the first place there does exist for this factor experimental evidence that points *prima facie* to the potential significance of pressure in nature. Secondly, observational evidence from a number of isolated areas can never be irrefragable because of the possible existence of forms distinguishable physiologically though not morphologically. (Cf. the recent work of Krumbiegel (1932) on a Carabid beetle, in which he found experimentally that the physiological distinctions between specimens from different areas were much more appreciable than their morphological differences.)

As regards the possible manner in which pressure could affect the organism it might be (*a*) mechanical, rarefaction of the air weakening the powers of flight, or (*b*) physiological. Regarding (*a*) it may be remarked that most of the birds with which we have to deal are no more aerial than a wren: and those which spend most time on the wing, such as swifts and the big Falconidae, are notoriously free of the heavens to great heights.

The question of a physiological effect requires more attention. Pressure

is an obvious factor for experimental manipulation, and a small amount of laboratory work is on record. It is assumed that the most significant element in reduced atmospheric pressure is the shortage of oxygen.

Rosin (1928) subjected hens to a pressure so low as 230 mm. of mercury, which would be equivalent to the rarefaction at 27,000 ft., without obvious effects. The duration of the experiment was apparently short. We have no indication whether similar reduced pressure extended over weeks and months would result in a deterioration sufficient to unfit the bird for life under natural conditions. It seems, however, likely that an adult bird's adaptability to pressure is sufficiently wide to be without significance in the life zone we are dealing with. The conclusion is of course not strictly applicable to other species than domestic fowls, but the potentialities are sufficiently indicated.

The work of Riddle (1924) and Romanoff (1930) provides evidence that embryonic birds may be much more sensitive to varying oxygen pressures than are adults. To increased pressures their adaptability is great enough to remove the possibility of this factor's significance out of the range of practical consideration. With regard to reduced pressures the indications appear to be otherwise. Unfortunately Riddle does not present his facts with all the clarity that one might wish. It seems, though it is not stated, that he secured his reduced oxygen pressures not by exposing the eggs to air under reduced pressure but by immersing them in an atmosphere richer in nitrogen and poorer in oxygen than is air. His conclusions are: "Many bird embryos in one or another stage of development require an atmosphere containing...not less than 15 per cent. of oxygen" (p. 360). "A concentration of 17·5 per cent. of oxygen during 24 hours kills...weak and older normal embryos....For the entire developmental period a concentration probably not less than 14·0 per cent. is required" (p. 361).

Romanoff found that growth stopped when the pressure (oxygen) was reduced by about 23 per cent.

Now it can be calculated that the partial pressures of oxygen in artificial atmospheres containing 17·5 and 15 per cent. of oxygen are equivalent to those encountered at about 5000 and 8800 ft. respectively above sea-level. Again, Romanoff's reduction of 23 per cent. is reached at about 7500 ft. In the fowl, then, we should expect to find a marked mortality in the shell at 5000 ft. and almost 100 per cent. mortality at 8000 ft. A somewhat surprising result.

It occurred to me that as Kenya Colony possesses poultry farms up to 8500 ft. above the sea, and thereby provides a series up to uniquely high altitudes, I might be in what Elton describes as the exhilarating position of finding a large-scale experiment already carried out. Mr T. G. Watson of the Division of Animal Industry, Department of Agriculture, Nairobi, very kindly interested himself in the question and collected data through the Kenya Poultry Club. As a result he wrote: "My general finding is that there is no

greater mortality at 8500 ft. than at 5000 ft. Even at the higher altitude 100 per cent. hatchings frequently occur." It is not of course suggested that anything equivalent to properly controlled experimental data was available from the farms, but nevertheless if the experimental results quoted had been reflected in Kenya practice the data from the altitudes received by Mr Watson should have shown a marked difference.

Two possible reasons occur to one for the incompatibility of the laboratory and the Kenya data.

a) The effect of a reduced oxygen pressure in an artificial atmosphere at normal pressure may be different physiologically from that of a reduced oxygen pressure in a correspondingly reduced atmospheric pressure, such as always occurs in nature. I am indebted to Mr F. J. Norman for pointing out that physiological work on plants supports this view (cf. Clements, F. E., 1931). In that case the laboratory work is not relevant to our problem.

b) A strain capable of withstanding reduced oxygen pressures might have been unconsciously selected in Kenya. Otherwise, if the experimental results are indeed applicable to natural conditions the poultry introduced into the Kenya Highlands would have failed to perpetuate themselves.

On the whole the conclusion is that changing pressure, the one direct concomitant of changing altitude, is not likely to be significant in bird distribution.

c) *Temperature.*

Although there is much evidence to show that birds survive an exceedingly wide range of temperature so long as food is available (cf. Rowan, 1929, p. 163 for sub-Arctic aviaries: Stanchinsky, 1927, for wild birds in Russia) it is a natural assumption, and one that has been repeatedly made, that birds' ranges may be affected by temperatures not approaching the lethal extremes. As a working hypothesis it is reasonable, but I have been able to find no references to experimental data in favour of it. The Oxford Bureau of Animal Population confirms the view I had formed from search in the agricultural library at Amani. But strictly physiological literature may contain some references. Moreover, when the hypothesis is applied to an area such as the Usambara Mountains it must be held to imply a fairly high degree of sensitivity on the part of birds. Thus, all the striking changes in the composition of the avifauna to be described later will be found to be effective within a life zone of 4000 ft. Within that range the annual mean temperature only varies locally about 7° C. (see Text-fig. 1). The difference between the winter minima is a little greater (about 9° C.), but between the summer maxima it is less.

The extent to which birds are sensitive to changes in temperature on this small scale, or to what elements of the variable temperatures encountered in nature they react, is quite uncertain. Hope was aroused by the title of a paper by Mitchell and Haines (1927) on "The critical temperature of the chicken." The critical temperature is defined as "the environmental tem-

perature at and below which the heat production of the fasting resting animal will increase to prevent a lowering of the body temperature." In the summary of the paper it is stated that the "average critical temperature was 62° F.," but "some of the individual birds appeared to show distinct differences in their reactions." On reading the paper it is found from Table III (p. 555) that the "probable location of the critical temperature" varies among the 12 birds used from "above 75° F." to "below 50°." If any conclusion whatsoever is permissible from such data it is that critical temperature is individual rather than specific.

With insects the daily range of temperature has been established to be a limiting factor as well as the mean maxima attained in the summer and the mean minima of the winter. In addition the entomologists have been able to recognise the existence of a "preferendum," i.e. the temperature that any given species of insect prefers. It is regarded as "probably one of the most potent factors influencing the ecological distribution of insects and their movements." The preferendum of an insect species can readily be ascertained. For if an insect is "placed so that a choice of several temperature conditions is possible it usually moves about for some time and finally rests in a certain temperature zone" (Uvarov, 1931, pp. 54–6). It is immeasurably easier to manipulate an ant in a long box with a source of heat at one end, than to manipulate, let us say, a bush-shrike in any controlled surroundings capable of yielding reliable data as to its preferences under natural conditions: nevertheless it is surprising that no attempt to ascertain whether birds exhibit specific preferenda appears to have been made.

"Daily range" is an element of natural temperature that has been shown to be of importance to insects. Whether it is significant where birds are concerned we do not know. The increasing difference between annual mean maxima and mean minima with altitude (cf. Text-fig. 2) would imply a concurrent increase in daily range. Detailed records of daily range at Usambara stations confirm this inference, but the nature of the vegetation is evidently a modifying factor. The daily range tends to be lower in a neighbourhood where evergreen rain forest is predominant, and higher in bare country. It is highest in desert and smallest of all in the "indoor" conditions under a canopy of evergreen forest. Thus, while daily range differences of possible significance exist between the "general" climates of altitudes and districts, such differences are even more clearly marked (and hence of greatest potential significance) between eco-climates existing within the same "general" climate. The point will be referred to again in the section on eco-climates.

Uvarov (1931, p. 122) quotes species of insects the range limit of which has been found by various workers to coincide with annual isotherms. Most ecologists will agree that no conception can be formed of how such a mean, in which all the extremes of the year have lost their identity, can impress itself on an organism. For example, an annual mean of 15° C. might equally

well exist with mean summer maxima of 25° C. and mean winter minima of 10° C., or with mean summer maxima of 35° C. and mean winter minima of −5° C. Two very different types of climate would thus be masked under a common isotherm. An example is afforded by a comparison of the climates of Lushoto (at 4800 ft. in the Usambaras and within 6° of the Equator) and of Deepwalls (at 1700 ft. in the Knysna district of South Africa, latitude 34° S.). The annual means agree within 1° C.: even the mean maxima of the three hottest months and the mean minima of the three coldest show the same close correspondence. But at Lushoto the temperature is never greater than 32° C., while at Deepwalls temperatures of 38° C. are recorded in five months of the year, with an absolute maximum of over 43° C. (Phillips, 1931).

Such considerations need not exclude the use of annual means as an index for comparing the climates of different localities so long as they are of the same type. But obviously if any argument is to be based on annual means the constitution of each needs to be examined.

It may be that birds suffer discomfort, much as human beings do, with high temperatures far below the potentially lethal. I observed in Egypt that the hoodie crows and the sparrows both opened their bills and gasped when the temperature reached about 35° C. It seems too that undue heat and cold may lower the vitality of warm-blooded animals without evoking definite pathological symptoms, and under natural selection any such disability would tend to exclude a species from the zone in which the summer maxima or winter minima consistently passed the bounds of its tolerance. A thoroughly abnormal drop in temperature at long intervals is likely to be less significant in restricting a species' range than a succession of temperatures that are only a little below the optimum. For the effects of a rare catastrophe would be transitory compared with those of a steady depressant.

All the above considerations have reference to the health or comfort of the individual and its direct reactions, reflex or voluntary. Among many insects, however, temperature exercises an extremely important indirect effect through the rate of reproduction. Chapman (1928) gives experimental grounds for believing that the effect on certain insects of a single degree difference in temperature may be measurable by the proportionate increase in the population. Thus "two closely related and competing species of beetles in controlled environments are present in varying proportions, the ratio of the two to each other being dependent on their curves of proportionate increase. The species with the higher proportionate rate of increase at high temperatures is dominant at high temperatures." The annual proportionate increase, or better, the biotic potential, of most insects is measured in thousands. The biotic potential of birds, especially tropical birds with their small broods, and comparatively slow generation is vastly less. The average clutch of most Tropical African birds is under three. Such birds on a basis of two broods a year would have a biotic potential of between four and six. It is true that the stimulation of

reproductive activity in birds by optimum temperature would probably not be so direct and marked as it is in insects, whose whole vital functions tend to be narrowly governed by temperature. But the possibility that the biotic potential of a bird may be susceptible to some specific optimum in temperature is not one that can be dismissed, because the smallest differences, e.g. between 4·9 and 5·0, could over a period of geological time be as effective in establishing the dominance of one competing species over another as the vastly larger index figures of insects.

If ultimately we are able to convince ourselves experimentally that the comparatively mild temperatures we are chiefly concerned with here are indeed of direct significance in determining bird distribution it may prove that the relationship is not of the kind that can be derived from the meteorological records usually published. Thus, on the analogy of other forms of life the possibility must be considered that some kind of summation effect may be significant, e.g. of the number of degree-hours above a temperature threshold which would probably be specific. Such an effect would tend to exaggerate small temperature differences. For example, if the threshold were at 20° C. and the temperature exceeded that figure for 7 hours a day the respective numbers of degree-hours available at 21 and 22° C. would be 7 and 14.

As regards temperature in general we may conclude that under our peculiar local conditions and within the abnormally small range we have to deal with, there may be no experimental data whatever to show that temperature is directly significant to birds, apart, that is, from its influence on biotic factors. But analogy, although admittedly not close, suggests the possibility of such marked and varied direct effects that we shall be justified in adopting the working hypothesis that some element of temperature may be significant. It follows that in the present stage of knowledge no ecological study can hope to include the really significant temperature data except by a lucky chance.

In the absence of any guide I shall assume that the mean maxima of the hottest months and the mean minima of the coldest are at least likely to be more illuminating than the annual mean temperatures, or even the annual mean maxima and minima.

(*f*) *Climatic factors—General.*

In the foregoing we have been concerned mainly with the potential direct effects of the various climatic factors on birds. We have found no reason to suppose that wind or pressure can be significant; we have considered that under the peculiar extreme local conditions light may be an effective factor; we have adopted the working hypothesis that some element of temperature may be significant; and if the whole question of humidity effects had been less wrapped in obscurity and difficulties it might have ranked with temperature. Accordingly, as complete temperature data as possible are always required, together with the extreme conditions of light intensity; and, although

we cannot in the least estimate their direct significance, a certain minimum of humidity data. Altitude will, of course, only be mentioned incidentally, the emphasis being constantly on the temperature gradient, not on the pressure.

It is necessary here to emphasise that even were direct effects of light, temperature and humidity demonstrated experimentally they might in nature be masked by indirect effects. For temperature and humidity are the factors that in combination primarily determine vegetation types, and, generally speaking, the vegetation type determines the light. It appears, then, that on observational data we can hardly hope to be able as a rule to isolate any one factor as of compelling significance in determining distribution, and it is important that in seeking to interpret such data we should continually bear in mind that climatic effects may be less direct than they appear, and the significant factors of every category more complicated and interdependent.

(3) *Subjective factors.*

To these factors we attribute the preferences and repulsions that we observe and cannot in our ignorance rationalise. And it may be well to recall at the outset that the psychology of birds is much more complicated than that of the invertebrates usually the subject of experimental manipulation.

In the opening sentence under "Direct biotic factors" I referred to "suitable food, nesting sites or nesting material." I followed many previous authors. The phrase has become almost a cliché. But the truth is that the use of the adjective "suitable" in that connection is merely question-begging. Fortified by a knowledge of dietetics we may be able to assure ourselves that certain fruits are "suitable" nourishment for a given bird which is known to be frugivorous. The bird may have different views, and it alone is the arbiter of what is and is not "suitable." The same difficulty is sometimes encountered with the more primitive races of mankind. The savage's views are in conflict with the dietetic expert's, and the savage is prepared to back his opinions with his life.

It is most exceptional for any species to be specific in its diet. As a result of the examination of over 80,000 bird stomachs in the course of 40 years by the United States Department of Agriculture, McAtee has come to the conclusion that "a discrimination in the choice of prey by birds is...non-existent" (reviewed by Uvarov, 1932). I have not been able to consult McAtee's book, but in view of such work as Swynnerton's (1919) it seems likely that the statement of this conclusion is a little extreme. The review quoted has provoked much subsequent discussion in the pages of *Nature*, where it appeared. But I think that most people who have done any stomach examination at all will agree that species tend to have a wide range of food. It appears that generally speaking a flycatcher will take anything on the wing that is small enough; a thrush, berries in addition to a wide range of invertebrate food,

both Arthropods and Gasteropods; a barbet a variety of fruit. At the same time experience of birds in aviaries leads one to realise that in certain circumstances they are capable of narrow selection. Thus a *Turacus fischeri* Rchw. and a *Buccanodon olivaceum* (Shelley) kept by me, show themselves critical towards certain of the varieties of banana bought from the local Africans. In general the birds' tastes agree with those of human beings, and astringent varieties are rejected: but distaste is also shown for a certain plantain type of banana which I regard as palatable. (The enormous range of banana varieties can hardly be realised in Europe, where the wholesale suppliers handle practically nothing but the one variety, Gros Michel).

If there is any strong taste preference for one particular food it can in the nature of things often be exercised during only a part of the year. Or the passionately desired food may be scarce and form only a relatively small part of the total bulk of food swallowed. (Incidentally, the significance of such an item of diet would not be revealed by stomach examination.) We have then to consider whether in such circumstances the occasional or seasonal occurrence of the specially prized food could be effective in limiting the bird perennially to the immediate neighbourhood of that food's occurrence. It sounds unlikely: but the case of *Gypohierax angolensis* (Gmel.), the vulturine fish-eagle, shows that it may operate even in a most unexpected type of bird. It has been shown elsewhere (Moreau, 1933) that in all probability the highly anomalous range of this eagle in Africa depends on that of the oil-palm (*Elaeis guineensis* Jacq.), the fruits of which are occasionally found in its stomach; and that the bird in East Africa keeps much more closely to the neighbourhood of oil-palms than its powers of flight would lead one to expect.

The choice of nesting materials is a similar difficult point. A given forest species is observed to build its nest of skeleton leaves and nothing else. Does it do so because this material is plentiful in the forest and readily lends itself to the construction of the specific type of nest? Or is it so unadaptable that if all other conditions were favourable an absence of skeleton leaves would prevent it from propagating its kind? The possibility that the use of nesting material may be highly and consciously selective is illustrated by certain well-known species—e.g. the chaffinch, which has been described, perhaps with undue anthropomorphism, as decorating its nest with taste and ingenuity.

Of still wider application and still more vague is the preference for particular associations, particular "kinds of country." For example, a species whose material necessities appear to be met by a supply of insects, of fibres, and of any inequality that will hold a nest, may be found only in the neighbourhood of rocks. A shrike that ranges through the canopy of the evergreen forest may never cross into the contiguous plantation trees. Here we seem to have a counterpart of the vague repulsion—"unhappiness"—felt by some

men born among hills when they encounter flat country: or by the Bedawin of the Egyptian deserts when they enter the Nile Valley[1].

Elton (1930, p. 54) gives a good example of an irrational preference of this type. On one islet Arctic terns were observed to avoid all patches of grass although they nested on other kinds of vegetation. This preference can hardly have had any biological significance, because elsewhere birds of the same species nested on islets completely covered with grass.

We may regard the invocation of subjective factors as a suspicious expedient to be used as sparingly as possible; as a last resort of ignorance; as a confession of despair: but so much appears to be explicable by no factors other than the subjective that we are forced to postulate their existence.

IV. Eco-climates[2].

An eco-climate has been defined as "the sum-total of meteorological factors within a habitat" (Uvarov, 1931, p. 128). It is mainly conditioned by the material components of the habitat and their mutual relations in space. The spatial extension of the eco-climate to be studied depends partly on the size of the organism and partly upon its mobility. Thus the eco-climate of a grub in a rotten log is small and comparatively homogeneous. Most eco-climates are more complicated, and for mobile creatures consist rather of a complex of eco-climates inhabited by the individual for varying periods of time. Thus, a jerboa inhabits an eco-climate narrowly defined in all three dimensions while it is in its burrow, and a different one, limited in vertical extension by the creature's small stature but comparatively unlimited horizontally, when it is foraging on the surface of the desert.

The habitats of birds are of greater spatial extension than those of the animals just quoted, and their eco-climatic relations are more complicated. Apart from the fact that during its first few weeks an individual bird exists in the highly specialised eco-climate of the nest, during its adult life it frequents a more or less wide vertical range of the atmosphere and a variety of vegetation. A bird moving up and down between the ground and the branch of a tree passes through several climatic strata differing, as we shall see, to a surprising extent.

Temperatures, humidity, wind and light may all be modified in an eco-climate. Here for the sake of simplicity and also because it is *ex hypothesi* a factor of general importance, discussion will be practically confined to temperature. Throughout this discussion "temperature" refers to air temperature, radiant heat, such as is taken up by an unshaded object, being left out of

[1] Since this paper was accepted for publication, the work of **D. Lack** on "Habitat selection in birds" has appeared (*J. Animal Ecology*, 2, 239, 1933); this paper puts forward independently the same idea, and substantiates it by detailed evidence from birds on the Breckland forest plantations.

[2] Much of the theoretical basis of this section and the data on eco-climates from the North Temperate Zone are derived from **Geiger** (1927).

account. If any attempt were made to evaluate the temperature actually "felt" by an unshaded bird, fresh complications would be introduced because the heat absorption at the surface of the plumage must differ according to the colour and degree of glossiness, and the heat transmitted from the external surface to the skin must depend on the texture of the plumage. Actually in a bird the lungs may well be the surface most sensitive to air-temperatures. An immense number of measurements would be necessary to determine the climates frequented by a single bird in the course of a single day's activity. But the problem assumes more finite proportions if the underlying principles are considered for a moment.

The physical factors determining an eco-climate of the type inhabited by birds are (1) the proximity of surfaces capable of absorbing solar radiation by day and radiating heat at night, (2) the nature of the surfaces, (3) the freedom of air-movement, (4) the presence of shade. Air in close proximity to an unsheltered surface is hotter by day and cooler by night than perfectly "open" air is. The denser the surface the greater the day temperature and as a rule the greater the daily range, i.e. the more extreme the eco-climate. The canopy of a forest and the upper part of a close stand of herbage both act as heat surfaces, but not being so dense as an earth or a rock surface the eco-climate conditioned by them cannot be so extreme. The colour of the surface is important because the paler the colour the more heat is reflected; and of still greater importance is its degree of dryness. A surface capable of giving up water will not condition so extreme an eco-climate as a dry surface. Thus the transpiration of green grass will have a modifying effect on its eco-climate, which will be less extreme than with the same grass when it is withered. Restriction of air movement round heat surfaces assists the hot air to accumulate and makes for a more extreme climate: but where heat surfaces are absent it makes for a more equable eco-climate (e.g. in a burrow).

In nature some or all of these factors operating in modification of the "general" climate are effective simultaneously. They may exaggerate or they may cancel each other's effects. Moreover, in nature there are endless combinations of the eco-climatic factors in varying degrees of potency. Nevertheless, the general principles being accepted, it is now possible to particularise a little further.

Thus, it is clear that within any given "general" climate the most extreme eco-climate will be that encountered on the surface of bare ground. Probably the highest temperature of all will be experienced by a bird like *Thamnolea* moving about on naked rocks by day. (The actual surface temperature may exceed 60° C.) Again, at any given moment, assuming identical conditions of sun and shade for both birds, a lark working bare ground in the African bush by day would be exposed to an air temperature much higher than an *Anthoscopus* on a twig 6 ft. above its head. While we have no actual records of the temperature difference in these circumstances in Africa, data for tem-

Photo. E. A. A. R. S.

Phot. 1. Intermediate forest, exterior.

MOREAU—EAST AFRICAN BIRDS

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perate climates show that it would often exceed 10° C. That is equivalent to the difference involved in more than 5000 ft. of altitude.

The eco-climates conditioned by vegetation are the most important we have to deal with. They have already been mentioned under indirect biotic factors. It appears that within its immediate influence the same type of vegetation modifies the "general" climate in the same way irrespective of locality: or in other words we may expect to obtain from a systematic study a factor of modification expressed in numerical terms and approximately constant wherever the same type of vegetation occurs. In dealing with natural vegetation the major difficulty, not quite so great in plantations, must be to ensure that the vegetation under investigation is comparable to that for which the factor was calculated. And of course between any types selected there will in nature be complete transitional series.

We may have to wait a long time before such factors are available. Meanwhile we may indicate the direction in which the "general" climate appears to be modified for certain main vegetation types. For the last one it will be possible to produce numerical data, and tentatively a temperature modification factor:

(*a*) Low herbage—a few inches high.

(*b*) Taller herbage:

(i) Plants with broad leaves more or less horizontally disposed dominant.

(ii) Erect grasses dominant.

(*c*) Bushes.

The foregoing eco-climates are considered for unshaded situations. The presence of overhead shade tends in all cases towards equability. The tendency is exhibited in its extreme form with type (*d*) (ii) below.

(*d*) Evergreen forest.

(i) Canopy.

(ii) Interior.

(*a*) Low herbage will be hotter by day and cooler by night than the "general" climate. The heating effect will be greater when the vegetation is dry. This condition is usually encountered in the hot season, and the extreme nature of the low herbage eco-climate is thus exaggerated to the utmost.

(*b*) In herbage more than about a foot high at least two climatic layers are engendered.

(i) Plants with broad leaves horizontally disposed produce by day in their topmost few inches temperatures appreciably hotter (at least 3° C.) than the "open" air above, while close to the ground the temperature is lower than in the open. At night the entire temperature range in the vegetation is below

that of the open. (But with a transpiring organism the absence of air movement close to the ground might offset the biological consequences of the lower temperature.) In other words this type of vegetation produces a climate more extreme than the "general" in its topmost layers but in its lowest a climate that is if anything more equable and consistently cooler.

(ii) Erect grasses are at their tops hardly appreciably hotter by day than the open air, but the air temperature rises rapidly as the ground is approached (by as much as 4° C.) and there is no well-developed cool belt close to the ground as with type (*b*) (i). At night it is a little colder halfway down the stems than it is at either the top or the bottom of the grasses. Thus with the erect grass type of vegetation the eco-climate of the tips approximates to the "general" climate but that of the interior is more extreme, mainly in the direction of greater heat and most exaggerated in the dried-up conditions of the hot season.

This eco-climatic description is based on measurements in cornfields in Germany. It will be subject to some modification in accordance with the habit of the individual grasses dominant in any given stand. But the great heat inside tall grass is well known to anyone who has followed African paths through "Elephant Grass."

(*c*) Bush, if dense, tends to resemble type (*b*) (i) in being more extreme, hotter by day and cooler by night. The difference may be as great as 5° C. in both directions. (Based on unpublished data collected in Kenya by the Entomologist, East African Agricultural Research Station.) In fact, as might be expected, it appears that bush and herbage (*b*) (i) condition similar eco-climatic systems.

(*d*) (i) Forest canopy tends to be hotter by day and cooler by night than the "general climate" (cf. Geiger, *op. cit.*). In fact the eco-climatology of the canopy of a forest appears to be governed by the same principles as unshaded bush. But in downward passage through the canopy the eco-climate changes progressively to that diverging from the "general" climate in the opposite direction and described in the following subsection.

(ii) Evergreen forest undergrowth exists in an eco-climate much more equable than the "general" climate, perennially cooler, damper and darker. The degree of equability appears to depend primarily on the density of the canopy above. This eco-climate is of great interest because it houses a whole special fauna. No published data regarding the climate in the interior of a forest in Tropical Africa appear to be in existence. An attempt has therefore been made to obtain data in the Amani forests. The results of a year's records are omitted from this paper for reasons of space. It is hoped to publish them later.

Briefly, at 4 ft. above the ground in intermediate forest (3000 ft.) and in the somewhat lighter lowland forest (1150 ft.) (to be described botanically

Phot. 3. Intermediate forest, interior. Liana growth is well shown.

Photos. E.A.A.R.S.

Phot. 2. A track through lowland forest.

in my synecological study (*J. Ecology*, in press)), divergences from the "general" climate are, to the nearest 0·5° C., as follows:

In annual mean temperature	...	−2·0° C., −1·5° C.
In summer maxima	... ...	−4·0° C., −(3·0° C.)
In winter minima...	... ...	−0·5° C., 0° C.

Although, as already stated, we have no data from any other part of Tropical Africa, Phillips (1931) has investigated the climate in the evergreen forest at Knysna which is comparable with Usambara forest. He found the (annual) mean maxima under the canopy to be 3·3° C. less than outside and the mean minima to be practically the same in both sites.

On the three sets of data available we are justified in concluding that the divergence from the "general" climate inside forest resembling the types in question lies in reduction of maxima (and daily range). As it happens that the subtropical forest investigated is the most luxuriant in East Africa, it is probable that a modification factor of −4·0° C. in maxima will not be exceeded in East and South Africa. We should expect the factor to be bigger in the West African forest with an interlocked canopy as described by Chipp (1927). The range between −4·0 and −3·0° C. may be expected to cover most forests that are tall, evergreen and closed.

It follows from the foregoing that only a small proportion of the total avifauna actually inhabits the "general" climate. The birds that do so most nearly are those that live in open arboreal surroundings, e.g. the fork-tailed drongo, *Dicrurus adsimilis divaricatus* (Licht.) and the wood-hoopoe, *Phoeniculus purpureus marwitzi* (Rchw.)—to quote local races. A large proportion of the other open country species live in temperature conditions more extreme than the "general" climate: how much more extreme we have no definite data to decide. But almost certainly within tall grass the modification factor is above +4° C. in maxima. On the other hand we have found the corresponding factor for forest undergrowth to be −4° C. So that the difference between the maximum temperatures encountered by birds in the two habitats, which often occur in immediate proximity, is as much as that involved in at least 5000 ft. range of altitude.

It is to be noted that the temperature differentiation with altitude expresses itself primarily in the minima, which change, as shown in Text-fig. 2, twice as fast as the maxima: whereas the eco-climate temperature differentiation lies principally in the maxima. Excepting where local topography favours accumulation of cold-air drainage, it appears from what we have said above that whatever the nature of the habitat its minima as a rule diverge comparatively little from the "general" minima. It would follow from this that eco-climatic modification of temperature is not generally capable of completely counteracting altitudinal modification, or that the "general" climate of any given altitude could be duplicated in an eco-climate at another altitude. Thus,

for example, the forest eco-climate at 2000 ft. may agree with the "general" climate at 4000 ft. in maxima, but it cannot in minima.

These facts introduce somewhat new ideas. In the first place it appears that in the general course of their existence a great many birds are (largely owing to their small size) enveloped in much higher air temperatures than are human beings inhabiting the same locality. Birds may, and do, evade, the full eco-climatic extremes temporarily. Thus, by burying themselves at midday in the depths of a mass of vegetation of type (*b*) (i) they remove themselves from the immediate proximity of the heat surfaces. (As stated at the beginning of this section, sun temperatures are excluded from this discussion.) But none the less many species will during their periods of activity be fully exposed to the eco-climatic extreme of their habitat.

Secondly, the eco-climatic differences between habitats in immediate proximity may be of direct significance in distribution. We have accepted the working hypothesis that comparatively small differences in temperature may be effective in differentiating altitudinal life zones. The differences between contiguous habitats are of the same order. It follows that such habitats may be differentiated by their eco-climatic peculiarities no less than by their material physiognomy.

V. Summary.

This discussion is preliminary to an attempt to describe in as much significant detail as possible the distribution of the habitats of the birds of the Usambara, a mountainous area in East Tropical Africa. African ornithology has shown a very strong bias in favour of the geographical aspect. Little critical ecological work has been done and it has seemed desirable to investigate *de novo* the principles with reference to which local bird ecology should be worked out.

Rainfall (as affecting vegetation) and also temperature have been cited by certain workers as master factors in determining the distribution of African birds.

Altitude has generally been treated as of great importance, but not, it appears, in a critical spirit. On consideration it is evident that the two determinable concomitants of increasing altitude are decreasing temperature and decreasing pressure. The relation between pressure and altitude is practically fixed; but that between temperature and altitude is subject to considerable variation (Text-fig. 1). The frequent connection of altitude with increased absolute precipitation is fortuitous. But decreased temperature increases the effect of the same amount of precipitation. In fact temperature and humidity in conjunction determine vegetation, so that they are far from being independent factors. Annual mean temperatures are by no means always satisfactory indices of comparison. Apart from any other factor, climate tends

to become more extreme with increasing altitude, owing to the rapid fall in minima (Text-fig. 2).

The environmental factors of potential significance to birds are discussed under the heads biotic (direct and indirect) climatic, subjective. Direct biotic factors in the narrow sense are recognised as insufficient to account for observed peculiarities of distribution. Indirect biotic factors include the eco-climates produced in different vegetation types.

No records of experimental work on the direct effect of climatic factors on birds have been discovered except for pressure. These experimental results are discussed and reasons are given for rejecting their application under natural conditions. In the absence of experimental data for birds recent advances in insect ecology have been utilised as a guide to the potential significance of climatic factors, due allowance being made for the fundamental physiological difference between birds and insects.

As a result of discussion of the individual elements of climate, the hypothesis is adopted that temperature may be directly significant even under the equable local conditions; our ignorance of birds' reactions to humidity is too complete to justify a hypothesis: light may be significant under the extreme local conditions. But it is again emphasised that these factors are interdependent on each other and on vegetation.

Subjective factors are held to cover preferences that cannot be rationalised. Instances are given of such cases and the reality of subjective factors is recognised with reservations.

The term "eco-climate" is defined and the physical principles determining the nature and degree of the divergence from the "general" climate are indicated on the basis partly of meteorological data obtained from comparable vegetation types in the North Temperate Zone, and partly on actual measurements made in Africa. The eco-climates of several important African bird-habitats are sketched. Most of them are more extreme than the "general" climate, the difference lying mainly in the direction of higher day maxima. An exception to this general tendency is provided by eco-climates under overhead shade, of which by far the most important is the eco-climate under a canopy of evergreen forest. There the day maxima are from 3 to 4° C. below those of the "general" climate. In fact eco-climates contiguous vertically or horizontally may differ by 8° C. and even more in maxima: this difference is equivalent to that associated with at least 5000 ft. in altitude. It follows that on the hypothesis of the direct significance of temperature in bird distribution eco-climatic differences must have some significance in differentiating habitats.

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THE FIELD VOLE (*MICROTUS*) AS A LABORATORY ANIMAL

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(*With Plate IV.*)

I. Introduction.

In the course of recent investigations upon natural periodic fluctuations and diseases among wild voles (*Microtus*) in Great Britain, it was found essential to obtain precise information about the factors controlling breeding.

Accordingly an investigation was carried out during the years 1930 and 1931 by Dr John R. Baker and myself, with the aid of a grant from the Empire Marketing Board. One of the results of this work was the development of a technique for maintaining stocks of laboratory-bred voles. *Microtus* can now be easily bred and used for pathological or physiological work and so forms an important addition to the somewhat limited series of laboratory rodents already in use. At the same time, as a result of controlled one-factor experiments on the influence of light, temperature and food upon breeding, together with an extensive field enquiry into the natural breeding seasons of voles in three areas in Great Britain, it was discovered that length of day is probably the principal controlling factor in nature.

It should be mentioned that Bailey (1924), in the United States, has successfully bred *Microtus pennsylvanicus* in the laboratory over long periods; but since he was dealing with a larger species which differs in some ways from the British vole, his technique does not directly apply to the latter. The same is true of the work of Chappellier (1932) on the Continental vole (*Microtus arvalis*) which is still more different in its habits and physiology.

The vole stocks at Oxford have played an essential part in the laboratory study of natural epidemics, such as those in North Wales and Scotland in 1933 apparently caused by *Toxoplasma* infection, which were investigated by Findlay and Middleton (1934). Voles have now also been proved to be highly susceptible in the laboratory to a number of virus diseases, e.g. Rift Valley fever of man and domestic animals (Findlay, 1932), louping ill of sheep (Findlay and Elton, 1933), climatic bubo of man (Findlay, 1933), yellow fever (Findlay, 1934), and foot-and-mouth disease (Edwards, 1934).

The vole has an additional interest, since all existing laboratory stocks have been living under artificial conditions for only a few generations, while the usual types of laboratory rodents (white mice, rats, guinea-pigs, etc.) have

been domesticated for such countless generations that they have developed a number of characteristics by artificial selection. There is little possibility of such selection having had much effect on the vole stocks as yet.

There are supposed to be two races or subspecies of *Microtus* in Great Britain—*M. agrestis* (northern) and *M. hirtus* (southern). The existence and relations of the two are still very problematical. The stocks at Oxford are derived from the hills of North Wales and the Scottish lowlands, with some additions from Aberdeenshire and Oxfordshire. They have been referred to for convenience as *M. agrestis*. The question of these so-called races merits further study, since it is now possible to supplement systematic work on structural characters by experiments on physiology and susceptibility to different diseases.

The vole stocks are maintained by the Bureau of Animal Population under the direction of Charles Elton and the facilities of the Department of Zoology and Comparative Anatomy are used at present, with the kind permission of Prof. E. S. Goodrich, F.R.S.

II. Cages and their furniture.

The cages we have used are of two types designed by Elton in 1929: large ones for growing young stock and for storage purposes, and small ones for isolating single voles and for breeding purposes.

The large cage measures $19 \times 16 \times 14$ in. high (outside measurement) and is made of a framework of 1×1 in. batten with perforated zinc, $\frac{1}{8}$ in. gauge, attached in such a way as to leave no exposed wood inside to be gnawed, the bottom being galvanised sheet-iron. Fifteen youngsters or eight adults can be accommodated in one cage. The small cage is a box of thin $\frac{3}{8}$ in. unplaned wood covered on the outside with $\frac{3}{8}$ in. mesh wire-netting and is roughly the shape of a boot box, being $13 \times 9 \times 5$ in. deep (outside measurement). The lid, which fits over the top, is a framework of 1×1 in. batten with netting stretched over it. The floor has a sheet zinc tray covering it (see Pl. IV, phot. 2). The advantages over the usual type of mouse cage are (1) cheapness, (2) easy accessibility into the cage without disturbing the voles too much, (3) the fact that voles cannot escape by gnawing holes in the sides. It will hold three adult voles or a nesting female with young until weaning time. All woodwork in both types of cage is given two coats of creosote which is allowed to dry for at least a week.

Granulated peat moss (supplied by corn merchants) is used for litter and, as it has very good absorbent powers, a complete clean-out is only necessary about once a month if the corners are cleaned weekly. In the wild state, voles shed dung at random throughout their surface runways, but also have special places in which they deposit large quantities of dung. In captivity they can be taught to use $\frac{1}{4}$-lb. cocoa tins as lavatories. One is laid in the corner of the cage and some dung placed in it. By the aid of these lavatories, cleaning

out of cages could be left for six weeks to two months; but as flea larvae soon multiply in the litter and nesting material it is not recommended that one month should be exceeded.

When starting up new cages (in the case of the small ones) the floor is lightly dusted with "Izal" powder to discourage fleas, and between two and three large handfuls of peat moss are evenly distributed over it. Then some hay (about 30 gm.) screwed up into a tight bunch is put at one end; this will be shredded up into fine strands by the voles, some of it eaten and some of it made into nests. In the case of females, soft hay is better than coarse stubbly stuff, and a few grammes of dried grass cuttings gives them a good medium with which to start building straight away. For large cages use three or four times as much hay and litter. Never be afraid of having too much hay and rough grass in the cage; the voles will make runways all through it, and except when hungry or during activity periods (see Davis, 1933) they will keep out of sight beneath this layer.

III. Food.

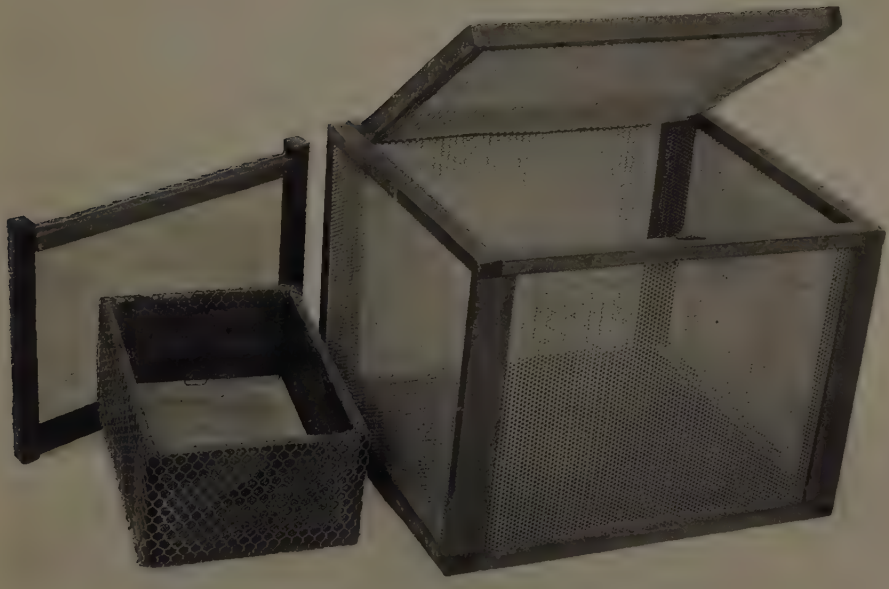
In the wild state voles eat mainly the stems, leaves and roots of rough grasses of all kinds (*Holcus*, *Molinia*, *Deschampsia*, etc.), also certain herbaceous plants. During a vole plague, large areas of rough grassland and pasture are completely laid waste, it being possible to lift up the dead grass and find a dense intricate system of runways, nest holes and "lavatories." As in the wild state a vole eats nearly its own weight of fresh green food in a day, in captivity it is laborious to give this large quantity of fresh grass, so that mangolds or carrots, hay, and mixed corn are given as well.

The daily ration for a vole of 30 gm. is approximately:

10 gm. fresh cut grass,
6 gm. mangold (carrot or turnip when mangold is unobtainable).
3 gm. mixed corn (composed of equal parts of wheat, barley, oats and maize).

Once a week about 20 gm. of hay are put into the cage and some of the old hay taken out. In the large cages the food is just dropped in. In the small ones the grass is not put in but laid loosely on the wire netting of the lid and is pulled through by the voles as required; in this way an excess is easily removed next day and it does not get fouled or trampled before it is eaten. When large numbers of cages are being dealt with and it is not possible to observe each vole daily, this method acts as a good indicator of the health of the population at a glance, for most if not all, of the grass, should have disappeared. The rest of the food is placed inside as in the large cages. Experiments have been conducted during the last four months to find out whether cod-liver oil could be substituted for the food elements contained in fresh-cut grass. It had previously been found that voles do not live successfully without

Phot. 1. Adult field vole (*Microtus agrestis*).



Phot. 2. Cages used for breeding field voles in the laboratory.

fresh green food. The experiments have so far proved quite successful both for living and breeding, and the cod-liver oil promises to save much labour and to make it easier to breed and keep voles in town laboratories. Fuller details and confirmation of these preliminary experiments will be published later.

IV. Mating, nesting, weaning and storing.

It has been shown (Baker and Ranson, 1933 *a* and *b*) that light and heat are the principal controlling factors of the breeding season of voles, and that a temperature in excess of 15° C. and 15 hours of natural or artificial light per day are necessary if maximum breeding is desired.

In the presence of females, males will not live together, but invariably fight to the death, so that the stock of breeding males has to be kept in separate small cages and mated to two females at a time. Until the temper of each individual male is known, and to guard against death by fighting, it is best to put the male in the mating cage after the females have been in residence for about 12–24 hours; this gives the females time to settle down and claim the cage as their territory and the excessive pugnacity of the male is thereby balanced. Although a little fighting is almost unavoidable, the females will not be bullied as is the case when the male is put in first.

If breeding is attempted in large cages, putting four to six females with one male, the same procedure applies except that when females become pregnant and are removed, new females must not be put in to take their place or they will very often be bullied and bitten to death by the other members of the "harem." The difficulty can be got over either by waiting till all the females are pregnant—this wastes space rather when the numbers become low—or by starting another cage with the remaining few and some fresh females to make up the number and treating them as a new unit, adding a fresh male later on. This procedure quite overcomes the complex troubles which arise out of the strong territory instincts present in voles in captivity.

The gestation period of voles is 21 days. Up to eight young are produced at a time, the average number being about four per litter. Unlike white mice, the vole will not rear its young in a nest containing any other families: consequently, when a female is found to be pregnant it has to be removed from the mating cage and placed by itself in a small cage containing a good surplus of nesting material pushed up at one end of the cage. If after about 24 hours the female has made no effort to start building but has spread the hay all over the cage, the hay must be scraped together again into a bundle and pushed back to one end of the cage. This does not often happen, but when it does, and is allowed to remain so, the resulting nest is very shoddy and thin and the vole will probably eat the young when born. Even if an apparently good nest is being made, a watch must be kept to see that it is not too thin on top, for to rear a family successfully the nest must be thick and dark inside. It

does not matter if the nest is opened and the young handled or examined so long as the damage is partially repaired and some more material thrown on top to cover the hole completely and make it dark again inside. In cases where it is necessary to handle or examine the young several times a day, a nest box about 4 × 4 in. with a hinged lid and an entrance hole in one side is useful. This can be stuffed full of hay and dry grass, and when the nest is made the top removed so that only the wooden lid remains. When this is lifted up, easy access to the middle of the nest is immediately possible; but for ordinary breeding purposes this is quite unnecessary and only increases labour and expense.

In a small family of two or three the young can be weaned from an age of 12 days on, but it is usually better to leave them a bit longer, as early weaning acts as a big check on their growth. If weaned at 14 days their quick development is assured. Also the parent female is given a little longer to recover condition. The young males will take 6 weeks to 2 months to become sexually mature, but the young females become perforate in as short a time as 20 days from birth. No fertile matings have taken place in the laboratory in less than 30 days from birth, but from evidence collected during the dissection of 2500 wild voles (Baker and Ranson, 1933), it was concluded that in the case of the female, fertile mating can take place about a week after leaving the nest, i.e. about 21 days from birth.

In the wild state during the height of the breeding season the female has an oestrus period directly after the birth of the young and will copulate again at once, so that a continual increase can occur every 21 days. It is not possible to breed at this rate in the laboratory stock owing to the difficulty of knowing exactly when the young are born and taking the female away without the young dying, for if a male is added to the nesting cage it will destroy the nest and eat the young. The most successful method of weaning is to remove the female and leave the young in the nest for 3 or 4 days when they can be transferred to the growing cages and kept in batches of ten to fifteen. The parent female is put into one of the breeding cages straight away. During the growing period it is essential that an excess of food should always be present, especially coarse hay and rough grass.

V. Handling, diagnosing pregnancy, and transport.

A very different technique is needed for handling voles than for white mice. The necessary grip is more comparable with that used for white rats. The procedure is as follows: When the lid is removed from a cage in most cases nothing but litter will be seen. Disturb this until the vole appears, place the left hand with spread fingers over it, completely covering it and pressing it firmly on to the floor of the cage; now slide the hand slowly towards you until the back and shoulders of the vole are visible between the spread fingers, and with the thumb and first finger of the right hand grasp the loose skin at

the back of the neck till it stretches fairly tightly across the throat and draw it out from beneath the left hand. The body must be steadied with the second and third fingers of the right hand by pressing them forward against the back, while an examination is made. The vole will usually make very little effort to turn round and bite, but there is always this possibility on the first few occasions, and they can rarely be handled at once with impunity in the careless way white mice can be handled.

Occasionally one has to deal with a vole which is apparently untamable and which will attempt to escape on every possible occasion. A rather more cautious procedure is necessary when handling such voles, but they are fortunately quite rare. From this elaborate description it might be inferred that voles are difficult to handle; generally speaking this is not so, and the technique can be mastered in a few days. After a week or two, most of the stock become so used to one that they will remain on the open palm without being held at all, and if the hand is moved up and down at the rate of about two beats per second they will sit quite rigid for long periods and the beat can be reduced to just perceptible motion. During 1933, handling on an average about a hundred voles a week, I have not been bitten once!

Pregnancy can be determined at a very early stage by gently pinching the abdomen with the thumb against the first finger resting across the back, when after a little experience both horns of the uterus and the rectum and the kidneys can easily be felt. The embryos are most readily felt when they are about 4 mm. in diameter or of about 12–14 days' development. I have diagnosed pregnancy at 5 days after conception by this method, although at that early stage the swellings are barely visible on dissection.

For transport we use the small cages roped together in tiers of four or five, with six voles per cage; but the whole of the cage is packed loosely with hay in which the voles can make runways and be out of the light. Also it absorbs the shocks incidental to rail or road transport. A large excess of food is put in, and a board or a sheet of thick brown paper is put over the lid of the top cage to avoid the unwelcome attention of fellow-travellers who might put in injurious food. If the voles are to be more than 24 hours in transit the number per cage should be reduced to four and more food put in. Wild voles are commonly sent distances of over 300 miles by train, and will survive without harm for at least 16 hours. We have little experience of sending voles longer distances, but would suggest large zinc-lined boxes with plenty of ventilation holes, peat moss at least 1 in. deep on the floor, and the whole box filled three-quarters full with tightly packed hay. A close-fitting solid zinc-lined lid with a lock and hinges, and cabbage or lettuce leaves substituted for fresh grass, would also be desirable.

VI. Summary.

The possibilities of extending the use of *Microtus agrestis*, the field vole, as a new laboratory animal are discussed and a technique for keeping and breeding them is described.

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THE ROOK POPULATION OF WEST GLOUCESTERSHIRE

By W. B. YAPP.

(With one Map in the Text.)

In the winter of 1932–3 a primary survey of the rookeries[1] of a portion of West Gloucestershire was carried out. In the spring of 1933 this was extended and a census of the nests was made.

I. The area.

The area investigated is roughly a rectangle, bounded on the east by the main Gloucester-Bristol road (A 38) from Berkeleyheath via Milburyheath to Filton, and then by the bypass (B 4056, B 4055, A 4018, B 4468) to Hotwells: on the south by the river Avon from Hotwells to its mouth: on the west by the river Severn to Sheperdine: and on the north by a country lane through Hill to Ham, and thence by B 4068 through Berkeley to Berkeleyheath.

The western part consists of an alluvial plain on the banks of the Severn, making up about half the area, and having an almost uniform height above sea-level of about 20 ft. Rising up from this on the east is undulating country with a maximum height of 351 ft. above sea-level, the underlying rock being almost entirely Rhaetic. There is a little Trias and some Carboniferous limestone exposed. The high ground is mostly pasture, but contains some arable land, and many houses with parkland and fox coverts, while the plain consists almost entirely of pasture, the fields being separated by rhines. There are numbers of hedgerow elms all over the area, so that nowhere is there any considerable region which is without suitable trees for rooks' nests. About $7\frac{1}{2}$ sq. miles in the south is within the boundaries of the city of Bristol. No allowance has been made for this in calculating densities, as most of it is agricultural land, and the rest is open suburb containing two rookeries.

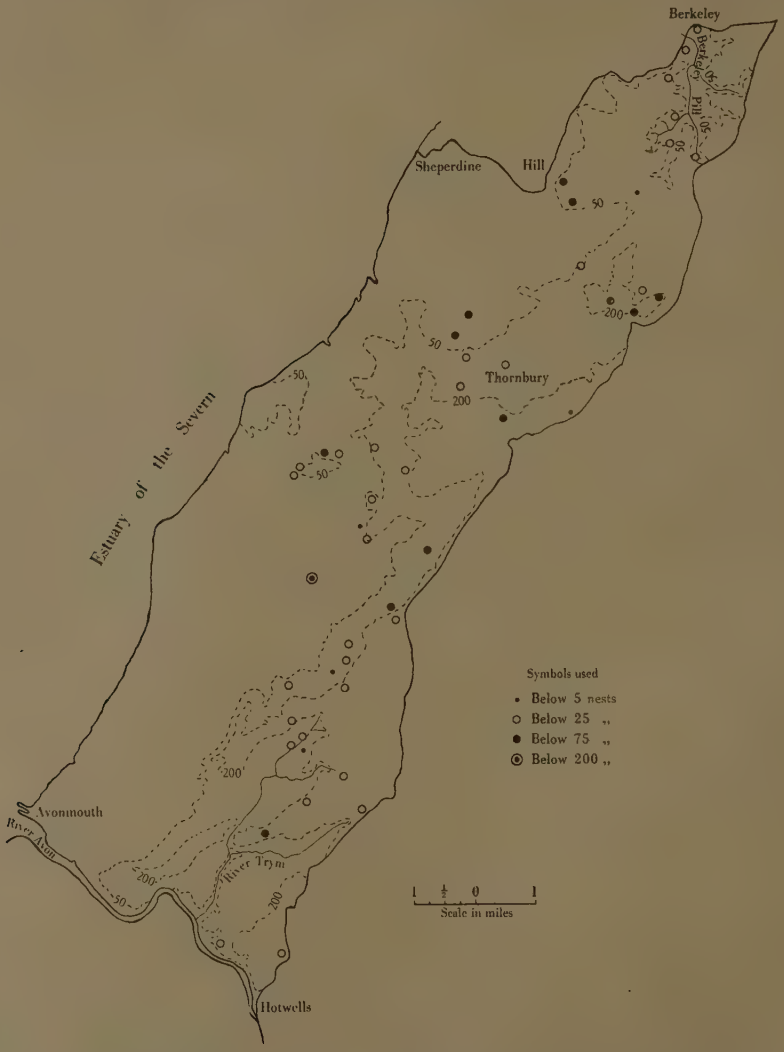
II. Possible errors.

There is a number of possible sources of error in the work.

(1) All the rookeries may not have been located. It is not claimed that every tree in the area was searched for nests, but it is not likely that any large rookeries were missed. Not all large isolated nests were examined, but all those which were belonged to carrion crows, and therefore no single nests were included in the count. Some doubt exists as to the status of one pair of nests, and three groups of three nests each at which no birds were seen. These are included in the census.

[1] *Corvus frugilegus* L.

(2) The birds might not have finished building. The error here is likely to be small, as counting was done from April 17th to 24th, after the young were hatched.



Map showing the distribution of rookeries in West Gloucestershire. Contours at 50 and 200 ft. Principal streams shown. Based upon the Ordnance Survey Map, with the sanction of the Controller of H.M. Stationery Office.

(3) Nests might have been destroyed. No evidence was obtained of this except in one case, where village children had done some damage on Easter

Monday. The figure used in this case is that given me by a local man who had previously counted the nests.

(4) There might be error in the actual counting. Probably in large numbers the possibility of missing a nest is balanced by the possibility of counting the same nest twice. In small rookeries there is no likely error.

III. RESULTS.

The total area investigated is 65·5 sq. miles, and the total number of nests 1009, which were considered for convenience as being in fifty rookeries. A full list of these has been deposited with the Oxford Bird Census.

The nearest area for which figures as to the use of the land could be obtained was the Petty Sessional Divisions of Thornbury and Berkeley. It is probably justifiable to assume that the proportions of crops would be the same for these as for the area surveyed, and densities have been worked out on this assumption. The date of the agricultural statistics used is June 4th, 1932.

Nests per sq. mile	15·4
Nests per sq. mile of agricultural land (crops and grass) ...	16·7
Rooks per acre of cereals (wheat, barley, oats, mixed corn beans and peas)	1·40
Rooks per acre of cereals, roots and potatoes	1·05
Rooks per acre of total arable land, including bare fallow	0·42
Acres of agricultural land per nest	38·5

IV. DISCUSSION.

Several factors have been suggested as influencing the distribution of rooks' nests; their application to the present data is discussed below.

(1) *Water.* There are no nests near the tidal rivers Avon and Severn which border the area on the south and west. The only other streams marked on the one-inch Ordnance map are the Berkeley Pill in the extreme north-east, and the Trym, which sometimes dries up in summer, in the south. There is no conspicuous grouping of rookeries round these. The flat land near the Severn has water-filled ditches (marked on the Ordnance map) along most of the hedges, but rookeries are few in this part. It is possible to find fresh water in the form of ponds near every rookery, but this is natural in agricultural land.

(2) *Buildings.* It has been said, e.g. by Wynne (1932) that there is a tendency for rooks to nest near buildings, but so far as I know no test of nearness has been published. The nests in the present area are distributed as follows:

Very close to human habitations	371
About 100 yards away from them	168
Much more than 100 yards away	470

(3) *Geology.* Apart from the lower density on the alluvial plain (see below) there is no obvious connection with geological formations, but probably the areas of Trias and Carboniferous are not large enough for conclusions to be drawn.

(4) *Altitude.* The nests are distributed as follows:

Below 50 ft., density	...	9·2 nests per sq. mile.
From 50 to 200 ft.,	...	18·9 nests per sq. mile.
Above 200 ft.,	...	26·5 nests per sq. mile.

The absence of nests from the low-lying ground is very striking, and I can see no reason to account for it unless it be the small amount of arable land. There seems to be a tendency, more obvious on the ground than on the map, for rookeries to be on the slopes of hills.

(5) *Trees.* By far the majority—78 per cent.—of the nests were in elms, but this may merely be because the elm is the commonest tree. There were 19 per cent. in oaks, all situated in compact copses, and the remaining 3 per cent. were in beech, sycamore, Scots pine, larch and one or two unidentified species.

(6) *Competition.* Lapwings, gulls, and woodpigeons are few in the breeding season, but much commoner in winter. There are relatively many carrion crows on the low lying land, but no estimate of their numbers was made.

(7) *Distance apart of rookeries.* There is no evidence for the suggestion that rookeries tend to be one mile apart.

V. Summary.

1. The density of rooks' nests in West Gloucestershire is 15·4 per sq. mile.

2. There is a low density on the flat land near the Severn, possibly connected with the small amount of arable land.

3. Otherwise the distribution seems to have no connection with altitude, water or human habitations.

VI. Acknowledgments.

I wish to thank the Statistical Branch of the Ministry of Agriculture and Fisheries, and the Justices' Clerks of Thornbury and Berkeley, for supplying me with information as to crops and areas: my father and sister for providing me with cars and for much patient driving: and Mr J. E. Clegg for checking my calculations.

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HABITAT DISTRIBUTION IN CERTAIN ICELANDIC BIRDS

By DAVID LACK, B.A.

I. Introduction.

This paper may be regarded as a continuation of my previous communication on habitat distribution in birds (Lack, **7**). To save repetition, the reader must refer to the earlier paper, especially for the arguments concerning the psychological factors influencing bird distribution. The present paper is based on observations made in Iceland from July 7th to July 24th, 1933, by the three members of the Cambridge East Greenland Expedition (see Roberts, **12**; Lack and Roberts, **8**). A few hours were spent in the Vestmannaeyjar and four days on the island of Grímsey. On the mainland the itinerary included Reykjavik, Gryla, Gullfoss, Laugarvatn, Þingvallir, Kaldidalur, Reykholt, Blöndrós, Langidalur, Akureyri and Myvatn, which provided representative localities in the south-west, the centre and the north of Iceland. The observations have been supplemented by reference to Congreve and Freme (**2**), Hachisuka (**3**), Jourdain (**5**), Roberts (**11**) and Slater (**13**).

The writer's thanks are due to Magnus Björnson of Reykjavik for further information on Icelandic distributions, and to Hugh Wormald for the note on young Harlequins. He is deeply indebted to his two companions, G. C. L. Bertram and B. B. Roberts, who share with him responsibility for the field observations in this paper, and who subsequently offered many useful criticisms on the views expressed. In the field the previous experiences of Roberts (**10**, **11**) among the people and birds of south-east Iceland were especially valuable. Dr H. L. Lack has also given valuable criticism during the preparation of the paper.

It is not intended to present a complete ecological survey of Icelandic birds, though such was attempted in the field. The distribution of certain species, often certain aspects only of their distribution, has been alone described.

II. The small Passerines.

Seven species of small Passerine bird breed regularly in Iceland. Their distribution in the various types of habitat may be summarised as follows:

Marsh, and grass meadow land:	Meadow Pipit (*Anthus pratensis* (L.))
Moorland:	Meadow Pipit
Moorland with birch scrub:	Meadow Pipit Redwing (*Turdus musicus coburni* Sharpe)
Birch forest:	Redwing Redpoll (*Carduelis flammea islandica* Hantzsch)

Moorland with large rocks:	Meadow Pipit Wheatear (*Oenanthe oenanthe schiöleri* Salomonsen) Snow Bunting (*Plectrophenax nivalis insulae* Salomonsen)
Barren rocky areas:	Wheatear Snow Bunting
Moorland near farm houses:	Meadow Pipit White Wagtail (*Motacilla alba alba* L.)
Towns:	White Wagtail
Moorland with cliff gorge and rocks near a farm:	Meadow Pipit White Wagtail Redwing Wheatear Snow Bunting Wren (*Troglodytes troglodytes islandicus* Hartert)

What factors determined the presence or absence of each species in a given area? Food was clearly important in determining whether *any* Passerine bird could exist in an area. For example, many barren mountain heights provided good nesting grounds for the Snow Bunting, but none occurred there, presumably owing to the scarcity of food. But in determining *which* species occurred in the habitats included above, all of which contained sufficient food for at least one Passerine, the food factor seemed unimportant. All seven species have a rather similar diet, consisting of small insects of most orders, spiders and some vegetable matter. They differ somewhat in the proportions of each type of food taken, but, though more data are required, it appears that they tend to feed on the commonest insects available—see for instance the summaries of Jourdain (**6**). Roberts (**11**) in south-east Iceland found many species of land bird eating the same type of food.

The nesting sites of the seven species are as follows:

Species	Nesting site
Meadow Pipit	In vegetation on ground
Redwing	In thick vegetation, usually off the ground, or in cliff gorge or rock overhang
Redpoll	In thick vegetation, usually birch or willow, normally off the ground, sometimes on it
Wheatear	In rock crevice
Snow Bunting	In rock crevice
White Wagtail	In hole in cliff, cave or bank
Wren	Under rock overhang

It is apparent that the nesting site was in many cases closely correlated with the distribution. On typical moorland only the Meadow Pipit occurred, but where there were large rocks, which could not materially affect the food supply but provided rock crevices for nesting sites, the Wheatear and Snow Bunting occurred as well. On moorland with birch scrub the Redwing occurred. The birch introduced some new insects, but this was not the factor influencing the Redwing, since it occurred on moorland without birch scrub when there were cliffs or rocks with overhangs. The birch or rock overhang provided the bird with a nesting site. Again the absence of the Meadow Pipit from towns,

where the closely related White Wagtail, which has similar food and feeding habits, was common, can be correlated with the absence of the ground vegetation in which the former normally nests. The restriction of the Wren to areas with overhanging rock was very probably due to the nesting site factor, but the bird was scarce, so that it is unsafe to generalise. The White Wagtail was not found away from localities providing its nesting holes, though this was perhaps not the only factor restricting its distribution.

Interspecific competition for nesting sites and food is often assumed to be of great importance in bird distribution. This certainly did not seem to be so among the Iceland Passerine birds. There was no competition for nesting sites, since in many cases the requirements of the different species were different. Also, where each type of nesting site occurred at all, it usually occurred in great abundance, e.g. rock crevices, and there were more than sufficient to go round. The seven species eat much the same food, but we found no evidence for thinking that there was only just sufficient food to go round, and in such areas as Myvatn, with its vast swarms of Chironomid flies, the insect supply was certainly far in excess of the birds' needs. Further, the birds concerned occurred in each type of habitat which provided them with certain definite nesting requirements, irrespective of how many other Passerine species, all eating similar food, occurred in the same area. Food competition was therefore insignificant. Where the moorland came up to a town, the Meadow Pipit was replaced by the White Wagtail, but the Wagtail did not *drive* the Pipit out from the towns, nor the Pipit the Wagtail from the moorland. Where the moorland provided suitable nesting sites, both species occurred side by side. The same applies to the replacement of the Meadow Pipit by the Wheatear in barren rocky areas. On moorland with rocks both occurred together. In one habitat (moorland with cliff gorge near a farm) which provided nesting sites for six species, they all nested in close proximity and fed over the same area.

In my previous paper I showed that the restriction of a bird to a particular type of nesting site is often due to a purely psychological factor and not to environmental necessity. Had it other instincts, there seems nothing to prevent Wheatear or Snow Bunting from nesting in vegetation like the Meadow Pipit, or the Meadow Pipit from selecting a rock crevice like the two former. Nevertheless each species adheres to its particular type of nesting site, which as a result is an important factor controlling distribution.

An interesting feature in Iceland is the strong tendency for the White Wagtail to occur near human dwellings. It was common in the towns, and there were one or two pairs round most of the farm-houses scattered over the country. Away from the houses it was scarce, but occurred in several cliff gorges. Possibly the neighbourhood of houses provides a larger insect food supply and possibly it supplies more crevices and holes suitable for nesting sites. But whatever the reason for the bird's association with buildings and stonework may be, it is interesting that it is also found on migration. The

species does not breed on St Kilda, but it passes through on migration, and in August 1931 T. H. Harrisson and the writer found the White Wagtail frequenting the houses just as in Iceland. It is also regular on passage at the Cambridge Sewage Farm, and here it is usually found on the stonework of a large drain running across the farm. The latter preference is shared by the passing Alpine and Rock Pipits (*Anthus spinoletta spinoletta* (Linn.) and *A. s. petrosus* (Mont.)) which, like the White Wagtail, normally breed in a rocky habitat; but it is not noticeable in the Meadow Pipits passing through on migration. To explain the latter cases one must invoke a psychological factor; food and breeding requirements are clearly ruled out. Habitat selection (*q.v.*) is not confined to the breeding season. But this opens a subject which is too large to be discussed further here.

III. The Ringed Plover.

Eleven species of wading bird breed in Iceland, on the coast, marsh and moorland, but the factors concerned in their distribution were not investigated in sufficient detail save in the case of the Ringed Plover (*Charadrius hiaticula hiaticula* L.), which was also investigated in East Greenland, where the same race breeds. The bird was common on most coasts, but also occurred some distance inland. Its restriction to stony areas for nesting was very marked. Thus in Jameson Land, East Greenland, it nested in the shingle beds of the rivers, was absent from the valleys round them which were covered with vegetation, and occurred on the barren heights above the valleys where stony ground was again found. This restriction was clearly not correlated with food, since the bird was not uncommonly seen feeding in areas well covered with vegetation and sometimes took its young there. All the nesting site that the bird has is a depression in the ground, which other types of habitat might supply. Perhaps the bird may benefit from nesting on stony ground, since its eggs are protectively coloured. But one cannot assume that the bird is conscious of this resemblance when selecting the site, especially since it not infrequently takes its young, which also resemble stony ground, on to vegetation, where they appear conspicuous. The selection of stony areas is best regarded as an example of habitat selection (see my previous paper) in this case perhaps correlated with an adaptation, the protective coloration of the eggs.

The barren heights of Jameson Land covered great stretches of country, but the Ringed Plover was found only where there was a small pool or stream, as Pedersen (9) also noted. This was clearly a case of limitation through food scarcity. Insect life was extremely scarce on the barren flats, but was common, as were also small Crustacea, where there were pools.

IV. THE SEA BIRDS.

The distribution of four members of the family Alcidae will be considered first. These all feed at sea and, at least on such remote islands as Grímsey, which is thirty miles from the nearest land, the food supply must be far in excess of their needs, and interspecific competition for food can be ruled out. Yet they do not occur indiscriminately all round the coast, and their absence from certain areas can clearly be correlated with their nesting sites, which are tabulated:

Common Guillemot (*Uria aalge* (Pont.)). On nearly vertical cliff on *open* ledges and tops of stacks.

Razorbill (*Alca torda* L.). On nearly vertical cliffs on *covered* ledges, and in shallow cracks. Usually there is rock immediately above the brooding bird's head but the bird is visible from outside, unlike the next two species.

Black Guillemot (*Uria grylle grylle* (L.)). In *deep* crevices in rock or débris, usually on lower part of *steep* cliffs.

Puffin (*Fratercula arctica arctica* Brehm). In *deep* holes usually on *gently* sloping cliffs or on flat-topped islets, both under rock and in turf.

Each species adheres to its particular type of nesting site, and is absent from coasts which do not supply it, often over large areas, where there may be abundant food. On the other hand, where a cliff supplies all four types of nesting site the four species often breed in close proximity. Interspecific competition for nesting sites is clearly insignificant, since each species adheres to its own type and there is little overlap. This adherence, as in the Passerine birds, must be psychological. There is no other factor apparent which can prevent the Common Guillemot from selecting a burrow or the Puffin an open ledge.

There is a similar phenomenon in certain Passerine birds. Closely allied species occupy distinct but adjoining habitats, with at most only a slight overlap, and the factor preventing overlap can only be psychological (see (7), p. 256). Presumably this differential habitat-selection is correlated with the evolutionary divergence of the four species, though the nature of the correlation is far from clear. It is interesting that the sea-birds parallel the Passerines in this respect, though they differ from the Passerines in that they feed outside the segregated habitats, which are only nesting areas, whereas most Passerines feed in the habitat in which they nest.

There is a small amount of overlap in the nesting habitats of the above four sea-birds. The Common Guillemot rarely selects a slightly covered ledge more typical of the Razorbill's site, and the Black Guillemot occasionally nests in rock débris at the foot of a cliff where one would rather have expected a Puffin. On Grímsey one was actually nesting right among Puffins. But such cases were exceptional in Iceland. (This slight overlap was also found in the habitats selected by closely allied Passerines.)

There are three other groups of sea birds in Iceland, the Petrels (Tubinares), the Gannets and Cormorants (Steganopodes), and the Gulls (Laridae). Each species has its particular type of nesting site and its coastal distribution

seemed largely limited by this factor. When the members of widely separated groups are compared, there is greater overlap in the type of site selected than in the above Alcidae. Thus the Kittiwake Gull (*Rissa tridactyla tridactyla* (L.)) often selected the same type of ledge as the Common Guillemot, the Fulmar Petrel (*Fulmarus glacialis glacialis* (L.)) at times used a ledge suited to the Kittiwake, the Manx Shearwater (*Puffinus puffinus* Brünn.) usually nests in burrows on turf slopes similar to those often occupied by the Puffin. This also parallels the situation among Passerine birds, in which the habitats of more remotely related forms often overlap. Whether there is ever competition for nesting sites between such species as Common Guillemot and Kittiwake is unknown.

The Gannet (*Sula bassana* L.) is especially interesting. It normally selects a broad flat ledge for nesting, but in addition to this it has a habitat preference for stacks and small islands. All the British colonies are on stacks or small islands as are all in Iceland save one on Grímsey. Some twenty years ago the stack where the birds bred on Grímsey collapsed, and there appears to be no other available. All the Gannets now nest on a cliff on the main island (where a few pairs bred before). This shows that a habitat preference which normally restricts distribution may be broken through when there are plenty of birds but insufficient normal nesting habitats, a point elaborated later.

V. The ducks.

The Icelandic ducks are found in three main types of habitat:

Lakes: Mallard (*Anas platyrhyncha subboschas* Br.)
Gadwall (*Anas strepera* L.)
Teal (*Anas crecca crecca* L.)
Wigeon (*Anas penelope* L.)
Pintail (*Anas acuta acuta* (L.))
Tufted (*Nyroca fuligula* (L.))
Scaup (*Nyroca marila marila* (L.))
Barrow's Goldeneye (*Bucephala albeola* (L.))
Long-tailed (*Clangula hyemalis* (L.))
Scoter (*Oidemia nigra nigra* (L.))
Red-breasted Merganser (*Mergus serrator* L.)

Swift flowing rivers: Harlequin (*Histrionicus histrionicus* (L.))
Barrow's Goldeneye
Red-breasted Merganser
Goosander (*Mergus merganser merganser* L.)
(Some of the lake species occurred in more sluggish rivers.)

Sea: Eider (*Somateria mollissima islandica* Br.)
(Some of the lake species, e.g. Scaup, Long-tailed, occurred in sea-lochs.)

On the lake Myvatn eleven species of duck, some of them closely allied, nest and feed in the same area. This is very different from the distribution of closely allied Passerines and Alcidae previously discussed. Red-breasted Merganser and Barrow's Goldeneye often nest in holes, but all the other species, and also the two former at times, utilise very similar sites, depressions in the rock or vegetation. Jourdain(6) and Slater(13) give data on the food of ducks, the latter writer from Iceland. The surface-feeding species, Mallard,

Gadwall, Teal, Wigeon, and Pintail eat mainly vegetable matter, though some animal food, mainly Mollusca and insect larvae, is taken, especially by the Pintail. The diving ducks, Tufted, Scaup, Barrow's Goldeneye, Long-tailed and Scoter eat mainly animal food, Mollusca, insect larvae etc., but also take some vegetable matter. The Red-breasted Merganser and Goosander feed almost exclusively on fish and their fry.

It is often assumed that in every animal community each animal more or less directly affects the rest, but this does not seem proved. On Myvatn, with its thousands of duck, we have no proof that there is competition between the different species, though their nesting sites and food are in many cases the same. We do not know whether the lake is supporting its maximum population with regard to either nesting sites or food. The numbers of one species may be quite independent of the numbers of the rest. This almost certainly applies to three of the species. Gadwall and Tufted first appeared only some thirty years ago, and have apparently been increasing ever since, and Barrow's Goldeneye is, according to Magnus Björnson, periodically affected by a disease which wipes out great numbers. (It is not known if the incidence of this disease is affected by the population density.) None of these three species need have attained its maximum density.

Conditions seem extremely favourable for duck on Myvatn, and most species are abundant. One result is that Barrow's Goldeneye cannot find sufficient normal nesting sites, a hole or burrow, and often nest in vegetation or among rocks. In other parts of Iceland, where the density is not so great, the birds almost invariably select a hole, and the presence of the latter may be an important factor controlling their distribution. This is another example of a bird breaking through a normally fixed preference (for a nesting site) where there are more individuals than typical sites present in a locality.

It is extremely difficult to see why the lake ducks, nearly all of which are marine in winter, should be almost exclusively freshwater in summer. In some species the young possibly require the type of food found in the lakes, but the Scaup and Long-tailed can and do breed successfully in the fjords at times. Perhaps the latter is another instance where habitat preference is broken through by pressure of numbers. The restriction of the Goosander to rivers is also difficult to understand, especially since the closely allied Red-breasted Merganser was not so restricted.

The Eider, normally confined to saltwater, occasionally bred in islets in rivers some miles from the sea. The bird also breeds on freshwater lakes on Bear Island (1). The young always seem to be taken to the sea on hatching, which perhaps controls the distance inland that the bird breeds. The bird's restriction to saltwater, where it feeds mainly on Lamellibranchs, is not understood. Nor is it known whether it feeds in freshwater when breeding there.

Another marked habitat preference is that of the Harlequin for swift flowing streams. It feeds almost exclusively on the larvae of Ephemeridae and

Phrygaenidae, which it obtains by turning over stones in the streams. This habit has rendered available a food supply not utilised by other ducks. Hugh Wormald of Dereham, Norfolk, who reared the young in captivity, writes "They are the most difficult of all ducks to rear....They appear to require small insects under stones, etc. They swim about poking their heads under every inequality in the ground under water and are extremely difficult to get to eat anything." They were eventually reared on "ants' eggs," fresh-water shrimps and insects. This specialised way of feeding is evidently fixed in the behaviour of the young, and presumably is the important factor in preventing the species from occurring in the habitats frequented by other Icelandic ducks, as shown by the difficulty in rearing it under the conditions normal for other ducks. It is not known whether there are any structural modifications correlated with this mode of feeding.

VI. Conclusions and Summary.

In the habitat distribution of the Icelandic birds described, much is unexplained, but the following factors appear important:

(*a*) *Food.*

Food is at times the factor limiting distribution, as shown by the Ringed Plover and the Snow Bunting. But though suitable and sufficient food is essential in determining whether any particular group of birds, such as the Passerines or Ducks, can exist in an area, it seems normally unimportant in determining which species of the particular group will occur there. The Harlequin provides a partial exception to this, being limited by a special feeding habit. This restriction is apparently correlated solely with the bird's behaviour.

(*b*) *Nesting site.*

Among the Passerines and sea birds, selection of a particular type of nesting site frequently limits their distribution. This restriction is usually only psychological, and, though normally fixed, is found to be overridden when there are more birds present than the typical sites can provide for. Under these circumstances the species does not appear to break right away from the typical site, but to select from the types available that most similar to the typical one. Hence the selection of a certain type of nesting site does not provide an absolute limit to the distribution of a bird in the way that food scarcity does. The bird is excluded from certain areas only so long as there are sufficient typical sites available somewhere.

(*c*) *Habitat selection.*

There are other examples of psychological factors limiting bird distribution besides those correlated with feeding and nesting sites, some of which were discussed in my previous paper, which included an hypothesis of habitat selection. Habitat selection may also be overridden by pressure of numbers,

instances of which have been given. Also Harrisson and Hollom (4) have shown that the Great Crested Grebe (*Podiceps cristatus cristatus* (L.)). when it was scarce in Britain, was restricted to the larger lakes. Now that it is common it occurs on many small ponds, in situations which would have amazed an earlier generation of naturalists. Hence the same considerations apply to the limitation of distribution by a habitat preference as apply to a nesting preference.

Four members of the Alcidae are an example of closely allied species of birds which occupy distinct but adjoining nesting habitats, as was previously shown for certain Passerines. Presumably the divergence of the four species is correlated with their differential habitat selection. Not all closely allied species of bird show this type of distribution. For example several closely allied species of Duck nest and feed in the same habitat in Iceland.

Habitat selection is not confined to the breeding season, as shown by the White Wagtail and Rock Pipit on migration.

(*d*) *Colonisation and competition.*

A species may be absent from an area which suits it in every way. In birds this is rarely because of a physical barrier, for they are mainly powerful fliers, and can cross barriers which would hold up for instance a mammal. Usually when a suitable area is uncolonised, it is because there are more than sufficient places suitable for the species elsewhere.

The number of birds in a given area depends primarily on the number of pairs available, which depends on the reproductive rate and the mortality. Each species has, in the first place, to be considered separately. If, as in some of the ducks, a species has arrived in a locality only of recent years, or if it is periodically destroyed by such factors as an epidemic disease or a hard winter, its breeding population may not be at the maximum permitted by food or nesting sites, and hence the species may not be in competition with other species in the same area, even though their requirements are similar. Considerations of a similar nature may apply to many birds. It is unsafe to assume *a priori* that a breeding population of birds in any area is at its maximum.

In certain areas the available nesting sites may be saturated. I was informed by a forester that the breeding population of the hole-nesting birds in the Stadtwald of Frankfurt-am-Main had increased by some 80 per cent. since the provision of an ample supply of nesting boxes on the trees. It may be noted that this was an "unnatural" environment: in a natural forest there would be many old trees, which would provide holes suitable for such species. The not infrequent British records of one species fighting with another for a nesting hole also suggest that competition for nesting sites occurs at times. But in other species, for instance the Icelandic Passerines and Alcidae, also most ground-nesting species elsewhere, there cannot be interspecific competition for nesting sites.

Finally, though it often seems to be assumed that the breeding population of birds is at the optimum or maximum permitted by food, this has never been proved for any natural habitat. Among the Icelandic Passerines and sea-birds interspecific competition for food was clearly insignificant and this perhaps applies to many other cases. Hence competition, for food or nesting sites, cannot be considered an important factor in bird distribution until further evidence is forthcoming.

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SOME NOTES ON THE NORTHERN ISLANDS OF LAKE VICTORIA

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(*With Plates V and VI and two folding Maps.*)

The facts given in sections II–V have been already published, those in the sixth section are for the most part here presented for the first time. It was thought that it would serve a useful purpose to bring together in this *Journal* some of the data which have been previously scattered in three distinct sets of publications. A very important paper by W. F. Fiske has also been included in the References, although no mention of it is made in the course of this article.

I. Preliminary.

The islands which form the subject of these notes lie between the parallels of 0·30′ N. and 0·30′ S., the Equator passing through Damba. The chain is near the coast, in some places only separated by a mile or two of water as at the western extremity of Buninga and the north-eastern point of Buvuma. Between these points the islands are divided, according to native law, into two groups, Sese and Buvuma, the former belonging to the province of Buganda, the latter to the Eastern Province. The Ba-Sese and the Bavuma people are notably different, and there is considerable difference between the flora and fauna on each side of the dividing line which passes between Damba and Dwaji.

The difference probably depends largely upon rainfall, which is much heavier at the western end of the chain. Bugalla island is stated to have a rainfall of about 80 in., whereas Masaka on the mainland to the west has only half that and Entebbe on the coast to the north, has not quite 60. Buvuma Isle has 55, but Jinja, on the mainland, only 46. These figures are taken from a chart prepared by the Uganda Survey Department in 1925. The prevailing wind being from the south-east, the north-west corner of the lake obtains the maximum rainfall, and the storms which come up from the lake discharge first upon the islands.

There is a curious and unusual feature about the storms on Sese, which occur often in the small hours of the morning and rarely in the afternoon. The normal time for rain in the tropics, 4 p.m., is observed quite often at Kampala and at Jinja, but very rarely indeed at Entebbe and not at all on Sese. Another feature of the climate of the western islands is the absence of a definite dry

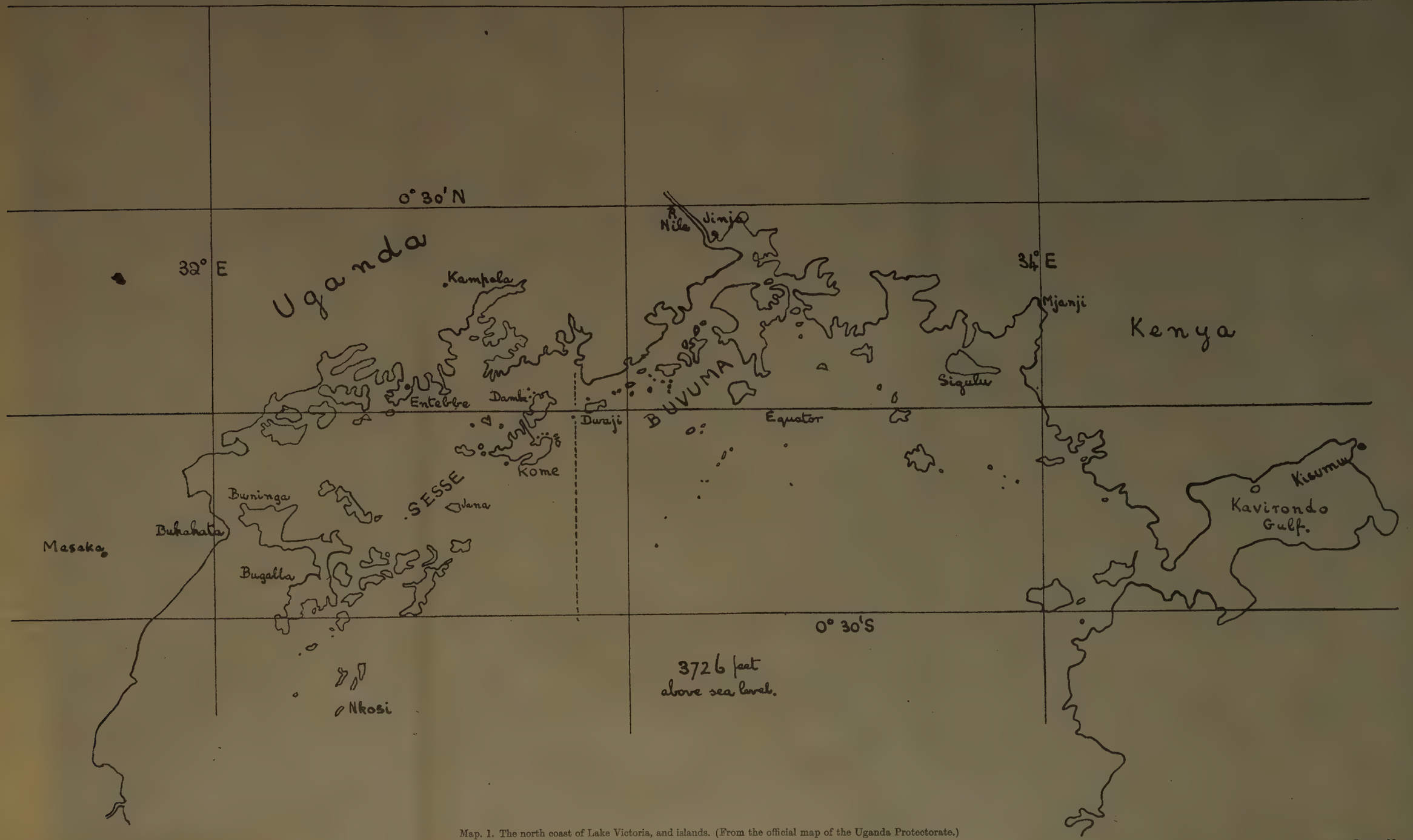
season, whereas on Buvuma, as at Jinja, the usual signs of a dry season are marked.

The writer resided on Damba isle from March to December, 1911, and on the north-east corner of Bugalla from March 1912 for twelve months. At the commencement of 1914 he had the great advantage of a tour among the smaller islands from Nsadzi to Wema with Mr W. F. Fiske, a field entomologist of great experience, and subsequently settled on Kome to continue investigations on the neighbouring small islands until September. In 1924 he was able to visit some of the islands lying off the Kavirondo (eastern) coast of the lake, and to experience the dry season there.

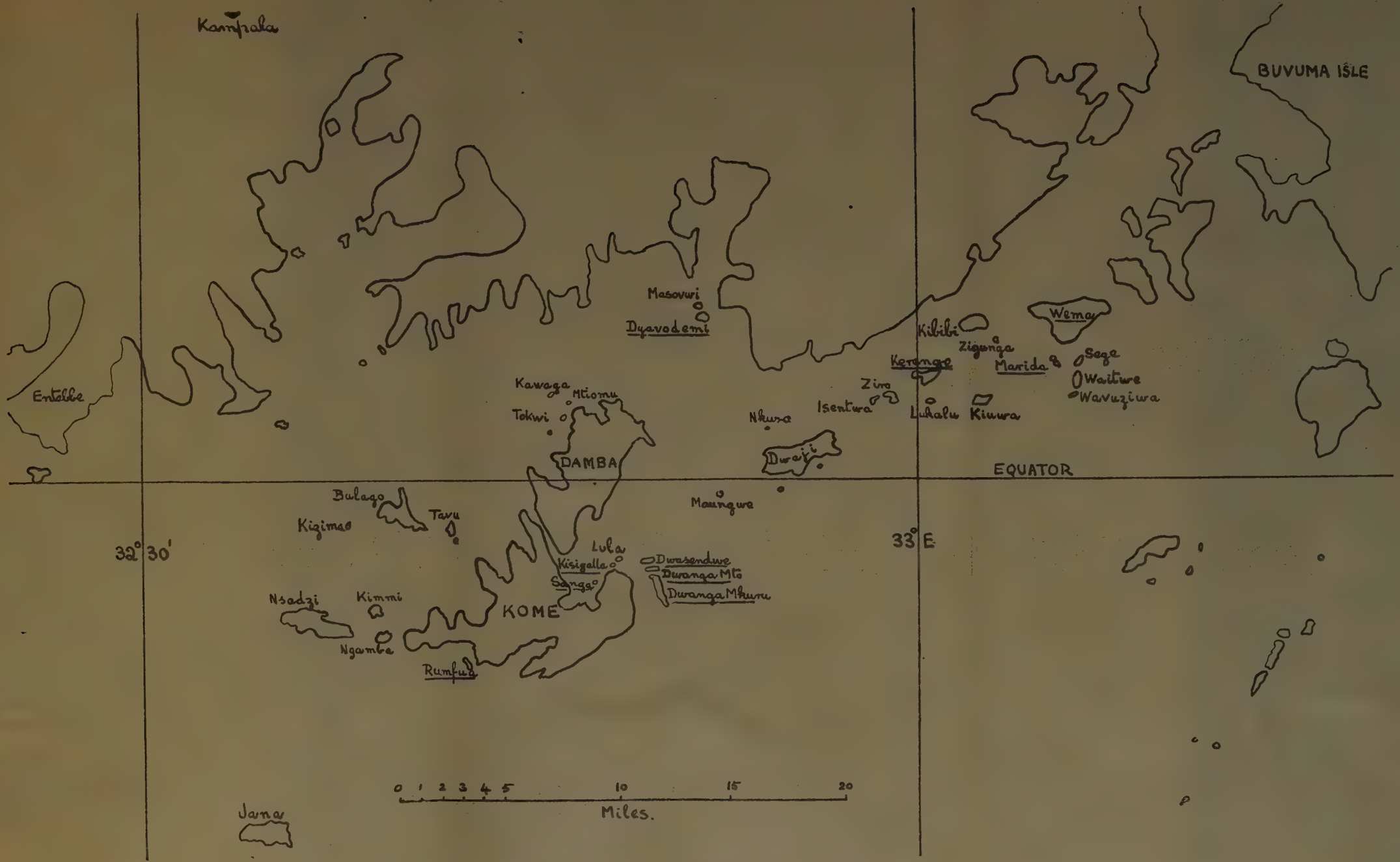
Unfortunately the writer had no botanical knowledge, and collected no data from which the differences in the islands could be studied. But, broadly speaking, while the western isles are clothed with thick forest wherever the soil can support it, which is usually around the coastline and on the lower slopes of the grassy hills, the eastern isles, and more especially those beyond Buvuma, have a xerophilous flora. Thorny shrubs and creepers, acacia trees, Candelabra Euphorbias, and such like are not found until one passes east of Dwaji, while on Bugalla there are tree ferns. Dr J. Burtt Davy has kindly told me that there is considerable affinity between the tree flora of the Lake Forests of Uganda and the rain forests of the coastal area of West Africa, from Nigeria to the Gold Coast. This is rendered the more striking by contrast with the tree flora of adjacent Kenya Colony and Tanganyika Territory. The writer, before visiting Damba, resided at Jinja in 1910 and became familiar with certain common flowering plants which were not seen on any of the Sesse group, but were first seen again during the eastward tour from Nsadzi when the Buvuma group was reached.

An interesting report on the Buvuma group of islands was made in 1925 by Mr T. D. Maitland, Government Botanist, to the Director of Agriculture, Uganda, who kindly sent the writer a copy. It is pointed out that the Buvuma group differ from Sese in that "Elephant grass" (*Pennisetum purpureum*) is absent from the former except for Dwaji Isle, which botanically is akin to Sese. The two palms so abundant in Sesse, *Phoenix reclinata* and *Raphia moubuttorum*, were not seen by Maitland on the Buvuma Isles, with one exception. Another characteristic of the Buvuma group was abundance of species of *Ipomaea*, especially a large woody species, not found on Sese. A tree that was very abundant on Damba and Kome in Sese, *Musanga smithii*, was not seen by Maitland in the Buvuma Isles.

The most beautiful of the islands are undoubtedly among the Sese archipelago; the numerous isles lying to the east of Bugalla, together with the irregular coastline of Bugalla itself form a panorama of surpassing beauty when seen from the central heights which rise to two or three hundred feet above the lake, and are usually covered with grass. Thick evergreen forest skirts the water's edge, and patches of forest on large islands may clothe the slopes. The



Map. 1. The north coast of Lake Victoria, and islands. (From the official map of the Uganda Protectorate.)



Map. 2. Some of the islands on a larger scale, Kome to Wema. (From the map in reference 3.)

Face p. 98

smaller isles are often densely covered with ferns, and the vegetation may vary from forest trees to a few bushes and large herbs. Illustrations of typical island scenery may be found in *A Naturalist on Lake Victoria* (Fisher Unwin, 1920).

There is very little papyrus among the islands except in the sheltered bay of the angle on the south side of Buninga-Bugalla, and on the north side of Sigulu, near Mjanji to the east.

II. Speke's Tragelaph.

This introduces the first subject of note in this paper, the presence on the islands of Speke's Tragelaph, or Situtunga antelope, which was found by Speke in 1862 in the district south of the Kagera river to the west of Lake Victoria, and was noted by him to be evidently adapted for life among papyrus swamps, with such long toes that "it could hardly walk on dry ground." The Situtunga is generally considered to be confined to papyrus swamps and appears to be a form specially adapted for that purpose.

It is therefore interesting that it is the only antelope on the islands, except for Bush-buck on Buvuma, and appears to be losing its special characteristics. When the writer lived in Sese during 1911–13 the antelope had become extremely plentiful, the native population having been removed wholesale some years before on account of the epidemic of sleeping sickness.

During daytime the Situtunga rest in the thickets and forest along the shore, and feed in the evenings along the edge of the forest and open grassland, browsing on shrubs such as *Alchornea cordata*, Bent., of which they are particularly fond. When disturbed they are seen to run very clumsily, so that the long feet are apparently not yet fully adapted to the change from papyrus swamps.

Yet the animals certainly swim from one island to another; in 1914 the island Ngamba was constantly visited and walked over, and, although no buck was ever seen, the bushes at the eastern side, opposite Kome on which the animal abounds, were browsed. Nsadzi island was stated by natives to have been free from Situtunga when it was inhabited, but in June 1914 the writer saw footprints of one. Major R. Meinertzhagen (7) visited Nkosi islet, the most southern and exposed of all the Sese group, and studied the Situtunga which abound there. He found that they showed distinct divergence from the mainland type, and even from those on other islands which differ less from the mainland animals. The feet have become less specialised, for they were found to be proportionately broader and in a young animal were no longer than might be expected in a young Bush-buck of the same age. The horns were also more like those of a Bush-buck, while the animals were larger than typical mainland forms.

The increased size of animals living crowded on a small island seems very remarkable. In 1928 the Game Warden of Uganda, Capt. C. R. S. Pitman,

D.S.O., M.C., estimated that the total number on the island was probably nearly 200: the island only measures about 200 acres in area! The island has been placed on the closed list under the Game Ordinance, so that further developments and changes should be unhampered by human interference. The writer visited the island in 1925, and again with the Game Warden in 1927, and the latter went again in 1928. An interesting point about the buck is that at that time they seemed loth to use the voice—the writer never heard the familiar bark, and Capt. Pitman, in spite of a definite drive having been arranged, only heard a sound on three occasions. Two troops of "an extremely pale race of *Cercopithecus pygerythrus*" were found, and these also seemed extremely loth to utter the usual warning cry when alarmed. During a visit of several days when the monkeys were frequently disturbed the alarm call was very seldom heard. Further notes on the fauna of Nkosi can be found in papers given in the references.

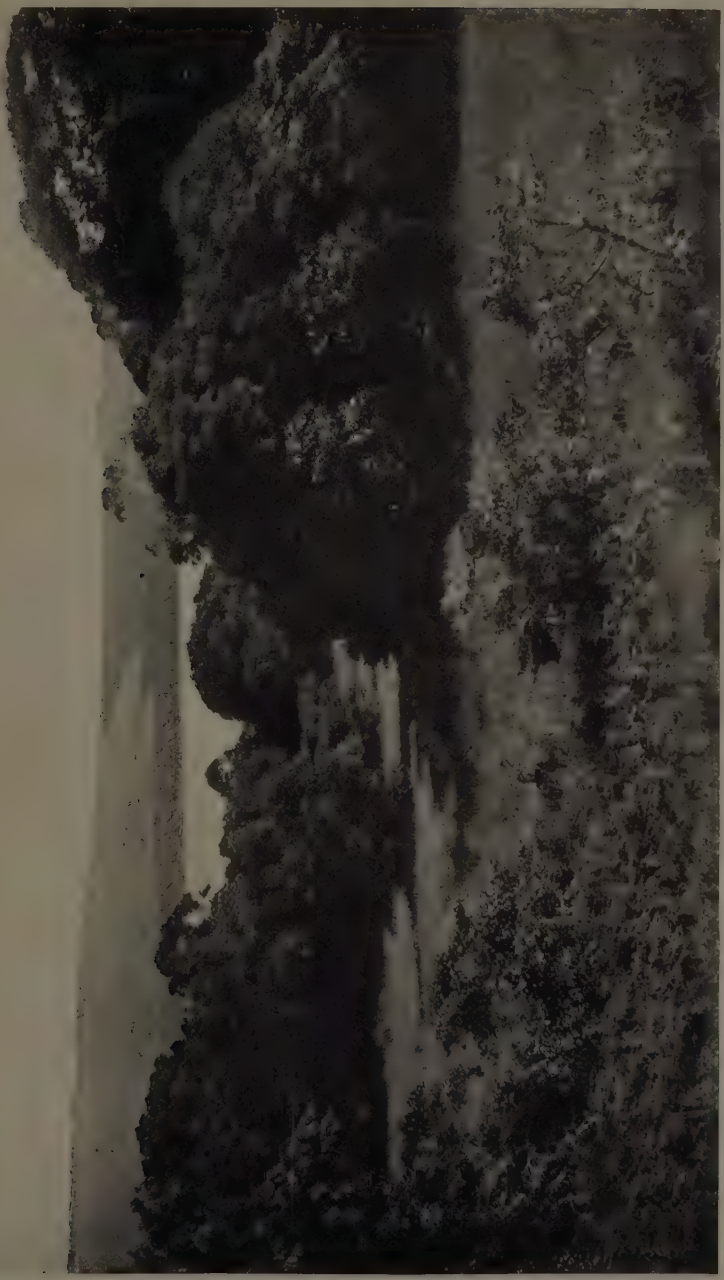
The increase in numbers of Situtunga on the larger islands in Sese began to show itself during the war years when Mr W. F. Fiske found that they were having a marked effect upon the flora. The species of undergrowth which they evidently preferred had been in places grazed to vanishing point, and the favourite bushes showed signs of severe browsing. It seems that owing to this there may have been lack of some necessary principle in the food available, for it was Fiske's experience that a large proportion of the animals had diseased coats and appeared "mangy."

In 1925 the writer revisited the area at the north-east corner of Bugalla Isle where he had spent fourteen months during 1912–13, and found an amazing difference. The Anonaceous undergrowth was so destroyed that individual plants could hardly be found: more remarkable still in an African forest, the ground was so bare of vegetation that one walked on dead leaves and twigs, and could see for a long distance along ground level. This clearing away of the undergrowth seemed to have had a profound effect upon the insect fauna.

III. Glossina.

Whereas during 1912–13 this area of coastal forest and the adjoining sandy beach had been the daily resort for study of the bionomics of *Glossina palpalis*, at the time of the visit in 1925 it was difficult to obtain a specimen. In March, 1912, the average catch for the month had been at the rate of thirty-six flies per fly-boy per hour: in March, 1925, only ten could be obtained on the same basis. This great difference is probably not solely attributable to the numerical increase of the buck, for other factors such as differences in lake level have their effects as well, but it is quite certain that clearance of the undergrowth must have had an adverse effect upon the tse-tse.

The relation of Situtunga to tse-tse on the islands is intimate. There is no doubt that *G. palpalis*, of all the species of tse-tse (which number about



(*From "A Naturalist in Lake Victoria," by permission of Messrs Bewn.*)

Phot. 1. North-east of Bugalla Isle. Parkland in foreground a typical haunt of Situtunga. At the back is central grassy highland with forest along a stream and bordering the lake. *Glossina palpalis* frequents the forest near the water.

twenty) is most adapted to feed upon reptilian blood, and examination of specimens from islands without any large mammalia show that a diet of purely reptilian blood is perfectly satisfactory to *palpalis*. But it prefers the blood of Situtunga to that of the hippopotamus, which frequently sleeps among the bushes near to the water. Examination of flies on Damba Island in 1911 showed that the proportions containing mammalian blood and non-mammalian blood were as twenty-one to seventy-nine; showing that, even though Situtunga were plentiful, their blood was one-third as popular as that of reptiles. Again, in 1914, blood from flies on two islands where Situtunga were found was in much the same proportions, viz. $M : N :: 25 : 75$.

On the other hand, flies from small islands on which the only large mammal was the hippopotamus showed $M : N :: 4 : 96$, so that 4 per cent. represents the value to the fly of hippopotamus for food and the difference between that figure and 21–25 per cent. represents the relative value of the Situtunga compared with the hippopotamus. It may be remarked that the protozoan trypanosome of the type generally similar to that which causes human sleeping sickness has been recovered from the Situtunga by Dr H. Lyndhurst Duke of the Human Trypanosomiasis Institute at Entebbe but not, so far as the writer is aware, from the hippopotamus.

It will have been noticed that even where mammalian blood is quite easily obtainable the fly seems to prefer reptilian blood.

This very probably explains its predilection for the open shore and banks of streams along which crocodiles and *Varanus* roam and bask. Tavu island was visited weekly by the writer from May 14th to August 18th, 1914, and at each visit the number of crocodiles basking on rocks along the coast was recorded, and then the number of *G. palpalis* that could be caught, the average for three localities on the island being taken. It was found that the number of males caught at any one visit bore a direct relation to the number of crocodiles that had previously been noted. It must be said here that since female tse-tse are not caught so readily as the more inquisitive males unless they desire to feed upon the observer, the number of *males*, as was first pointed out by W. F. Fiske, should be taken as the regular index. Since the real number of flies on this particular islet of less than one mile in diameter could hardly vary in such a way from week to week, and it is certain that they do not fly across the open water between islands, the explanation must be that the presence of the crocodiles caused large numbers of females to congregate for feeding, and the males assembled for the purpose of meeting the females.

Certain islands, notably Kimmi, were remarkable for the voracity of the tse-tse which would fly off to a visiting canoe and bite severely before the canoe had touched land: on other isles, such as Tavu, although large numbers could be captured they bit seldom. Comparison between the percentages of the sexes caught on different islands, the number of pupae found, and the stage of development of the pupae showed an inverse relation between these items.

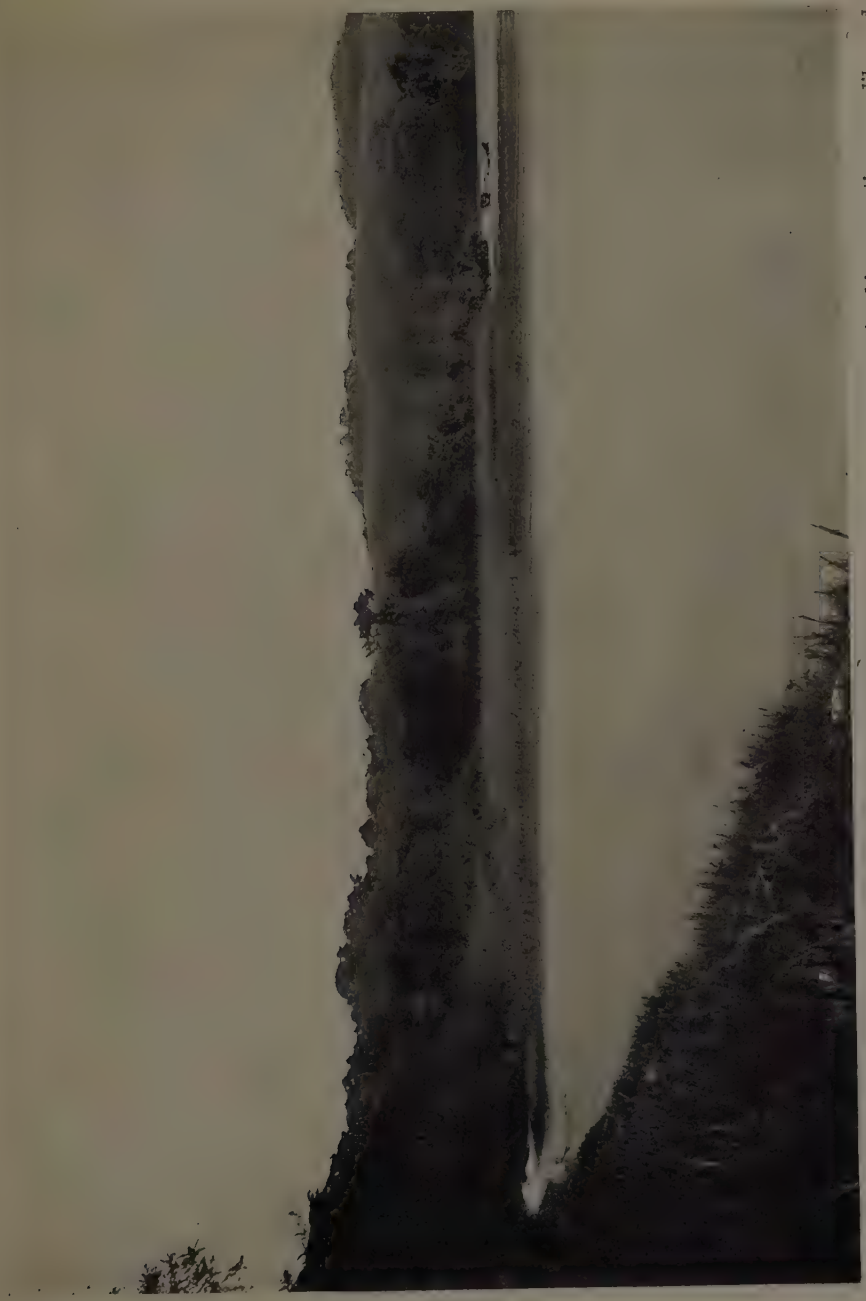
The Kimmi flies were extremely hungry so that there was an unusually high percentage of female flies among the captures; the number of pupae to be found was small and the pupae were shown by dissection to be mainly in an advanced state of development. The average female percentage for the island was 53 per cent., and at one locality reached the very unusual figure of 72 per cent.: the Kimmi average was 100 per cent. *above* the general average for nine islands examined, while the number of pupae was the same amount *below* the average. The flies on Tavu island showed the contrary state of affairs, with a female percentage of 80 per cent. *below* the average, never being higher than 24 per cent. with an average of 17 per cent.; the number of pupae deposited was 476 per cent. above the average, the number of pupae at an early stage of development on Kimmi was 30 per cent. below the average for nine islands, while on Tavu it was the same amount above that average.

When the abundance and hunger of *Glossina* on Kimmi were first noted, both crocodiles and *Varanus* were very scarce although their egg-shells were seen, which showed that at times they bred there. After the preliminary tour the writer settled on Bulago Isle, and visited Kimmi and other small isles at weekly intervals from April to August inclusive. During that time it was found that *Varanus* and crocodiles were frequently seen, and two nests of crocodiles' eggs were found: in May the percentage of females fell to about half what it had been in April, and never rose above nineteen per cent. until the observations were concluded owing to the outbreak of war: this was correlated with decrease of the intensity of the attacks of the fly as compared with earlier months.

These facts were interpreted to mean that starvation, as illustrated by high female percentage in the catch, implies slow reproduction, so that the proportion of pupae at an early stage of development is low. When the female flies can obtain plenty of food they are not caught so readily, and reproduction being rapid there is an increase in the number of pupae at an early stage of development.

It is generally accepted that *Glossina* deposits the mature larva in convenient places near to available sources of food supply so that the newly hatched fly can quickly find food. Thus it results that *palpalis* pupae, on Lake Victoria, are only found in numbers along the shore which is the chief haunt of the reptiles on which the fly feeds. The writer spent considerable time studying the "breeding-places" and concluded that the desiderata for *palpalis* are loose dry soil, well-shaded but with the surface thoroughly ventilated, within a few yards from high water mark, but beyond its reach.

The following observations show how carefully the female searches for the suitable conditions. A sandy area on which dense bushes grew seemed as if it should yield many pupae, but search was made without success. The ground was covered with débris of leaves and stalks owing to the depredations of great numbers of the larvae of a common *Acraea* butterfly feeding on the



Phot. 2. Part of Kirugu Isle: a sandy grass grown beach in foreground is a typical resort of grazing hippos, resting crocodiles and lizards (*Varanus*), which are bitten by *Glossina* emerging from the bushes along the water in the background.

bushes: consequently the surface of the sand was kept damp and mouldy. The search for pupae in the sand naturally led to displacement of the top layer of débris, and exposure of clean sand. A week later this spot was revisited and twenty-four freshly deposited pupae were found. This observation is also of interest as showing how one species may quite accidentally react upon the numbers of another.

Two other records showed how nicely the parent *palpalis* estimates the shade value of any particular spot as a repository for pupae. A thick tangle of young shoots of a species of Polygonaceae was found on a ridge of sand arching over the surface below. Eighty-eight pupae were found under the shelter of this, of which 91 per cent. were in a very early state of development, showing that they had only recently been deposited: only six empty puparia from which the fly had emerged were found. In other words, the locality had only just begun to provide conditions well suited to the pupae, and to be used as a breeding-place.

Exactly the opposite state of affairs was shown by a prostrate tree-trunk arching over the ground, which is a type of shelter often utilised by *Glossina* for pupae. There was a tangle of *Ipomaea* stems over the trunk, but half dead and leafless so as to provide little cover, though there was some new growth beginning. Search revealed forty-five pupae of which twenty-seven were dead: three were almost ready to hatch, while the other fifteen were in the earliest stage of development. It was obvious that at one time the creeper had provided enough shade to attract flies to deposit pupae, but having partly died it ceased to ward off the sun and many pupae had been killed. Subsequently, new growth attracted the fly again and fresh pupae were being deposited.

A papilionaceous tree which normally throws very thin shade had at one time been surrounded by rambling plants which had increased the shade density, but had recently died. No less than a hundred and thirty empty puparia were found from which the adult flies had emerged, and five dead pupae. Since the thinning of the shade no more pupae were being deposited.

The importance of good breeding-places to *palpalis* is shown by the diminution in numbers that follows an exceptionally heavy wet season when the lake level rises above the previous high-water mark. The unusually high lake penetrates to the old "raised-beaches" which, when covered with bush are such favourite breeding places. The pupae are drowned, and the deposit of débris renders the places just beyond unsuitable.

On the other hand, after a prolonged period of low level, the return of the lake to a former high level will result in old raised beaches, for long too far away from the water, being again rendered suitable. The writer saw a striking example of this in 1918. On the south-east coast of Kimmi isle in 1914 there was a flat strip of low-lying marshy land, covered with lush grass and appa-

rently left by recession of the lake from its former shore, as shown by a typical raised beach covered with the usual trees some hundred yards back.

This raised beach, which satisfied all the requirements of pupae save proximity to water, was never found to yield pupae in 1914. But in December 1918 the lake had risen so much that the water had returned to the old raised beach, which was then being utilised as a breeding ground, and numbers of pupae were found there.

IV. Spiders.

The comparative survey of many of the islands made on a tour with Mr W. F. Fiske, in January to March, 1914, showed that some of them were remarkable for the immense numbers of great spiders, probably a species of *Nephila* whose webs hung in successive sheets so close together that the owners of the inner webs seemed starved. It seemed possible that on such "Spider islands" (indicated on Map 2 by underlining the name) the numbers of *Glossina* must be affected, but no definite conclusion could be reached, as other factors such as breeding places complicate the situation. Large numbers of insects, including *Glossina*, were seen in the webs, but it seemed probable that the great clouds of "Lake-fly" (? Chironomidae) that reach the islands before and during the wet season and are caught in myriads by the webs must be an important source of food for these spiders.

Kerenge, Dyavodemi, and Ziro islands were "Spider islands" and had apparently good breeding grounds but the number of *palpalis* present was so much smaller than would have been expected that it seemed possible that the multitudes of webs may have been a limiting factor. Marida, another Spider-island, had superb breeding grounds, yet *Glossina* was very scarce there.

It was noted that on certain Spider islands the small birds which were usually found in the bushes and undergrowth were abnormally scarce, and it is possible that the dense sheets of web acted as a deterrent: on one occasion the writer found a Sunbird actually entangled. On such islands the scarcity of birds was sometimes correlated with abundance of the predaceous insects, Mantidae, and on one island the predaceous Asilid flies seemed far more abundant than is usual. Certain of the "Spider islands" were by no means unsuitable for butterflies and on at least one of these (Sanga) it was noted that the butterflies seemed to be flying unusually warily, and many of them had shreds of spider's web clinging to the wings.

V. Other insular features of the fauna.

Several islands which provided open areas of tussocky grass were characterised by abundance of a small rodent whose tunnels ran through the dense grass stems on which they obviously fed. Many interesting differences between neighbouring isles were noted, but as they have been previously published in full (**3**) the following will be given as an example.

There are three minute islands lying off the eastern point of Kome, close to the latter. Sanga was quite the most interesting of all the small islands seen: it was rocky, and covered with trees and ferns. Spiders were extremely abundant, birds very scarce, and Mantidae unusually abundant. The butterfly fauna was large for so small an island: thirty-five species were noted. The chief characteristic was abundance of "Skippers" (Hesperidae), which outnumbered any other group, for eleven species were counted. Among them the genus *Rhopalocampta* was very strongly represented, and the peacock-blue and green *Rh. chalybe* D. and H., has not been seen anywhere else in such numbers: it was an unforgettable sight as it flashed in the open sunlit spaces.

Lula was very different from Sanga, being clothed mainly with a common Euphorbiaceous shrub (*Alchornea*) and having no big trees. Birds, so lacking on Sanga, were seen, and a black and white Flycatcher, not seen on Sanga, was abundant. The large spiders and *Mantidae*, so plentiful on Sanga, were not noticed on Lula. The fifteen species of butterflies which were noted showed great differences from Sanga, for seven were Acraeines and only one a Hesperid.

Kisigalla, between the last two, was more like Sanga in its trees and ferns. Birds were quite plentiful, and the *Nephila* spider, although present, was not so abundant as on Sanga. Twenty-two species of butterflies were noted of which Lycaenidae, represented by eight, formed the largest group. Large numbers of a Scoliid wasp flying closely over the ground indicated the abundance, underground, of some species of Scarabaeid larva. A peculiarity was the presence of very large numbers of a large cream-coloured slug.

VI. Butterfly fauna.

The butterfly fauna of the islands having been studied more particularly than other groups of animals, some general points of interest are here brought together: the large collection has been finally arranged as a separate geographical entity in the Hope Department of the Oxford University Museum, available to all for further study.

Those species which show seasonal variation are especially interesting if what has been said of the climate is borne in mind. In Sese there is no real dry season, for there is some precipitation during every month. The Nymphaline genus *Precis* behaves in accordance with this, for the commonest species, *P. archesia*, to be found on every island that is large enough, was always in the wet-season form *pelasgis* Godt., except for one specimen taken in the centre of Bugalla Island, the largest of the Sese group, which was slightly transitional to the dry-season form *archesia* Cr. This specimen was taken in August 1929.

The species which shows the greatest degree of seasonal dimorphism, *Precis octavia*, appears most often in its pink wet-season form. It was only found in Sese on the largest isle, Bugalla, where twenty-five of the pink form *natalensis* Stgr. were taken, and only four of the blue dry-season form

sesamus Trim. These latter were captured on June 1st (two), June 17th, July 16th towards the close of the heaviest rains while wet-season forms were taken in January, February, March, June, July, August, September, and November.

A most remarkable capture was made on Wema Isle, well within the eastern drier group: a specimen of *Precis pelarga* of the form *harpyia* F., intermediate between wet and dry-season forms. No other specimen of this species was ever taken among the islands and it seems possible that it was a migrant from the adjoining mainland.

Pierinae such as the genus *Terias*, and *Satyrinae*, which show seasonal variation, were in accord with *Precis*: indeed one specimen of *Terias brigitta*, Cr., taken on Eastern Kome in the middle of the rains was noted by Dr F. A. Dixey, F.R.S. to be the "wettest" specimen of this species that he had ever seen. The few specimens of the Nymphaline *Byblia* that were taken were also all "wet" forms. The following point has not hitherto been brought especially before the notice of ecologists, although much has been made of it in writings on Mimicry:

The Acraeine genus *Planema* provides models for numerous forms of the Nymphaline genus *Pseudacraea*.

Different species of *Planema* are closely copied by different forms of *Pseudacraea eurytus* L., sex for sex, and when a *Planema* is alike in both sexes so also are the mimics.

Very large collections made of these at Entebbe on the mainland by Dr C. A. Wiggins had shown in 1909 that the Planemas greatly outnumbered Pseudacraeas, and that the latter were stable in their appearance, although an occasional very rare intermediate was found. But when the writer collected on Damba Isle in 1911 and for a longer period on Bugalla Isle in 1912–13 he found the reverse conditions; few Planemas and a much larger number of Pseudacraeas, which showed great variability with many intermediate forms. Kome Isle in 1914 provided the same fauna as Entebbe, the Pseudacraeas being relatively few and stable. But in 1918–19 when the writer again visited the same part of Kome Isle, the conditions were the reverse: there were more Pseudacraeas than Planemas and they were again more variable.

The fluctuations in the number of *Planema* and *Pseudacraea* are such as are familiar to an ecologist, but the interesting point is that when the numbers of models are sufficiently large the mimics are true to them, but if the mimics are much more numerous than the models they vary greatly, and intermediate forms are plentiful. It seems good evidence in favour of the working of natural selection to keep the mimetic resemblance up to standard in the presence of models numerous enough to have a protective value. But when models are numerically very inferior to their mimics a variation of the latter away from the mimetic appearance does not place the bearer at a disadvantage. Another piece of confirmatory evidence is that on different small islands the

prevailing species of *Planema* was different, and the appearance of the *Pseudacraea* was in accord with the prevailing *Planema*. A full account of these points will be found from the references. It may be argued that when islands are so close together, birds, which are held to be the selective agents, will surely fly across from one to another, so that the close adherence of one form to the appearance of its model on one small islet need not protect it against a visitor familiar with another type of model and mimic on its own island. But it is a fact that, judging by differences in call notes or song, the birds of one island tend to remain there, and perpetuate minor differences distinctly noticeable to the percipient ear. The writer knew very well the call notes of the commonest Bulbul and the Paradise flycatcher, and found distinct variations from one island to another, or even on different parts of a large island such as Bugalla. Thus it seems possible that there may be quite local selection.

Another point of interest in the fauna is the mixture of Eastern and Western forms. Uganda, though geographically considered as part of East Africa, has many western constituents in its fauna, and there are even slight differences perceptible between the eastern and western ends of the island chain.

Papilionidae. *Papilio rex*, which so beautifully mimics the Danaine *Tirumala* was only found on Buvuma Isle, where five were taken. Two were of the form *mimeticus* Rthsch. characteristic of Entebbe, its western limit, two of the form *commixtus* Auriv. transitional between the western *mimeticus* and the eastern *rex* Oberth., and one transitional to *commixtus*. This species is much commoner at Jinja, opposite Buvuma, than at Entebbe, and the forms on Buvuma seem slightly more eastern than the usual forms from Jinja, suggesting that they came from the east side of the mainland near Buvuma and not from the side facing Jinja. *Papilio cynorta* is very rare on the islands, and there is only one specimen of the female in the island collection, taken on Kome in 1929; this is the cream and brown form *peculiaris* Neave, characteristic of Uganda, and is the eastern form of the species which is black and white in West Africa. A large collection made by the writer in 1915 in a forest about thirty miles from the west coast of Lake Victoria, on the Anglo-German frontier, showed that the female *P. cynorta* there was invariably of the black and white western form. This rather suggests that the *cynorta* of the islands came from the mainland to the north rather than from the much closer mainland to the west.

Danainae. The genus *Amauris* shows decided difference between east and west. *A. niavius* is represented by forty-five specimens the characters of which are more of the western form *niavius* L., with less white, and by four which show more white and are transitional to the eastern and southern *dominicanus* Trim.

Another species, *A. damocles* is even more abundant. There are in the collection four specimens of the western *damocles* Beauv., though not in its fullest degree of darkness: one transitional to *psyttalea* Plötz., the common form in Uganda; twenty-one *psyttalea* and three transitional to the eastern form *damoclides* Stgr., with more white. A single specimen of the characteristically dark western species *A. hecate* Btlr., was taken at the eastern end of the Kome Isle.

Nymphalinae. The western influence is predominant; such species as *Euphaedra ruspina* Hew. and *Euptera elabontas* Hew. showing this well. *Pseudacraea boisduvali* is of the western form *boisduvali* Dbl., and among the many variants of *Pseudacraea eurytus* on Bugalla, was a female which approached very nearly to the typical western form *eurytus*, L. On the other hand, *Pseudacraea kuenowi* is of the eastern form *neumanni* Thurau.

The genus *Hypolimnas* often shows marked differentiation between west and east, and the species *dubia* from the islands is of interest. There are in the collection eight of the western form *dubia* Pal., one *anthedon*, Dbl., and one of the eastern *mima* Trim.; another is transitional from *anthedon* to the eastern *wahlbergi* Wallengr. *Precis terea* shows very distinct difference between eastern and western forms, and all the specimens seen or captured were of the western form *terea* Drury. *Precis octavia* is, on the contrary, always of the characteristic eastern type.

Acraeinae. The genus *Planema* is represented by seven species on the islands; they show no difference in their geographical type from those of the mainland. Uganda is the eastern limit of several species, and they appear in different guise from the typical western forms, but do not to any important degree go east of Uganda. One truly eastern species, however, *Planema aganice* in its eastern form *montana* Btlr., seems to have only recently established itself in the neighbourhood of Entebbe in Uganda, which so far as the writer knows is its western limit, and only reached Damba and Kome Isles after 1911: it has not yet been taken on any isle west of the Kome group. It is abundant in Kenya Colony and Tanganyika Territory: the large collections made by Dr C. A. Wiggins at Entebbe in 1909–11 showed it to be extremely scarce there, for out of a total of 1405 Planemas and Pseudacraeas captured to show the mimetic relationship there were only nine *aganice montana*. During 1911 the writer collected on Damba Isle and found no specimen.

But in 1914 *aganice* was found abundantly on Kome, and by 1928 was abundant at Entebbe, and on all the islands of the Kome group. This seems to be an example of a recent invasion by a typically East African species.

Acraea zetes is a species with well marked western and eastern forms, and out of the one hundred and seventy specimens in the collection twenty-eight were of the form *menippe* Dr., of western appearance, while one hundred and forty-two were of the form *jalema* Godt., more eastern in type.

Acraea egina Cr., has provided an interesting pale form, *alba* Eltr., on Bugalla Island which approaches a form *medea* Cr., apparently confined to Prince's Island in the Gulf of Guinea. This form *alba* is followed by the Bugalla race of *Pseudacraea boisduvali* Dbl.

It is shown elsewhere (**14**) that this species of *Pseudacraea* is of western rather than eastern type on the Sese Isles.

Lycaenidae on the whole showed a western bias; species characteristically West African such as *Spalgis pilos* H.Dr., were found, while it cannot be said that any typically East African species was taken on the islands.

Hesperidae, to judge by the specimens in the collection, showed some interesting differences between the islands of the Sese group to the west of Kome, and Kome, and the isles east of it.

Thus the peacock-blue *Rhopalocampta chalybe* D. and H. was not taken east of the islet of Sanga on which it was so abundant.

Andronymus leander Plotz. was found in great abundance on Kerenge Island, and was also taken on Wema. It agrees with specimens from Entebbe and the forests west of the lake in being a distinctly different race from the West African examples of the species. It is larger and more heavily marked with bright orange yellow. But although it occurs on the mainland to the west of Bugalla it has not been taken on any island west of Kerenge.

Pardaleodes incerta Snell, was not found west of the Kome group, *Osmodes* was represented by *O. argenteiguttata* Mab., on Bugalla, but from Kome eastwards by *O. thops* Holl.

The genus *Acleros* does not appear in the collections from Bugalla or Kome, but on Bulago, Sanga and other isles to the east of Kome two species occurred. *Hypoleucis tripunctata* Mab., was first seen, proceeding eastwards on the tour, on Sanga, and subsequently on Damba, the Dwanga group, and Wema. During the fourteen months on Bugalla the writer never saw it.

The genus *Eagris*, and the closely allied *Sarangesa*, it is interesting to note, are not recorded from the western Sese isles: Bulago being their western limit. In the writer's experience these species are found in drier countries, and one species of *Sarangesa* is well known to take shelter during the hot dry season in the holes of the "Aard-vark" (*Orycteropus*).

Species of *Celaenorhinus* also were characteristic of the eastern islands.

VII. Summary.

1. This paper is the result of notes made on sundry subjects when the writer was engaged in studying the bionomics of *Glossina palpalis* on the chain of islands parallel with the north coast of Lake Victoria.

2. After a preliminary account of the islands and their climate, and a few notes on the flora, the increase of Speke's Tragelaph or Situtunga as a result of the depopulation of the islands is discussed. The changes brought about by

their unchecked multiplication are described, and the differences in the buck themselves from their mainland neighbours.

3. Some work on the food-preferences of *Glossina*, and the influence of abundance of food on their rate of breeding, follow; observations are quoted showing how carefully the parent fly searches for the appropriate environment in which to deposit the larva.

4. The fourth section deals with insular abundance of a large species of spider (*Nephila*) and its effect upon the rest of the fauna: other insular features characteristic of three small islands lying close together are then mentioned.

5. The last section gives a brief account of the more interesting facts emerging from a study of a large collection of butterflies made at different times upon some of the islands, showing that there is a great difference between the faunas of the ends of the chain.

6. References are appended.

REFERENCES.

The following publications, by the writer unless otherwise stated, contain the records from which this paper has been compiled. In addition, a mass of detail will be found in the important paper cited as Reference 6.

A. *Bionomics of* Glossina palpalis *Rob.-Des.*

(1) "Progress report on investigations into the bionomics of *Glossina palpalis*." Reports of the Sleeping Sickness Commission of the Royal Society, 1912, 12, 79–111.

(2) "Second report on the bionomics of *Glossina fuscipes* (*palpalis*) of Uganda." Ibid. 1913. 14, 1–37.

(3) "Third, fourth, and fifth reports on the bionomics of *Glossina palpalis* on (the) shores of Lake Victoria." Ibid. 1919, 17, 1–101.

(4) "Report on a test of a method of attacking *Glossina* by artificial breeding-places." Bull. Ent. Res. 1923, 13, 443–5.

(5) "Report on an investigation into the epidemiology of Sleeping Sickness in Central Kavirondo, Kenya Colony." Ibid. 1924, 15, 187–208.

(6) **W. F. Fiske.** "Investigations into the bionomics of *Glossina palpalis*." Ibid. 1919–20, 10, 347–403.

B. *Speke's Tragelaph, or Situtunga.*

(7) **R. Meinertzhagen.** "Notes on the Situtunga or Marsh Antelope of the Sesse Isles, Lake Victoria, Nyanza." Proc. Zool. Soc. Lond. 1916, 375–81.

(8) "Speke's Tragelaph on the Sesse Isles of Lake Victoria." Ibid. 1925, 1423–30.

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(10) **C. R. S. Pitman.** "Notes on the vertebrate fauna of Nkosi Island, Lake Victoria." Ibid. 1929, 133–46.

C. *Butterflies.*

(11) "*Pseudacraea eurytus hobleyi*, Neave, its forms and its models on Bugalla Island, Lake Victoria, with other members of the same combination." Trans. Ent. Soc. Lond. 1913 (1913–14), 606–45.

(12) "*Pseudacraea eurytus hobleyi*, its forms and its models on the islands of Lake Victoria, and the bearing of the facts on the explanation of mimicry by Natural Selection." Ibid. 1920 (1920–21), 84–98.

(13) "*Pseudacraea eurytus* and its models in Eastern Uganda." Ibid. 1923 (1923–24), 469–91.

(14) "*Pseudacraea boisduvali*, Doubl., and its models, with especial reference to Bugalla Isle." Ibid. 1913 (1913–14), 646–55.

(15) "Attacks of birds on butterflies." Ibid. 1933, 81, 1021.

THE WINTER FOOD OF BROWN TROUT (*SALMO TRUTTA* L.)

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I. Introduction.

While many accounts of the food of brown trout (*Salmo trutta* L.) during the spring and summer months exist, the food during the winter period is less well known, the principal source of the records having been trout caught by anglers during the fishing season. An opportunity having arisen for the study of the food during the winter, the following account refers principally to that period and is offered as a continuation of the work of Pentelow (**1**) who has given a systematic account of material from the Rivers Tees and Itchen, collected during March to September, and who reviews the literature of the subject.

II. Materials and methods.

The material was obtained from a fishery on the upper part of the River Test, in Hampshire. The contents of the stomachs of 100 brown trout were examined, from fish which had been removed from the river on account of their being considered disadvantageous to the fishery. The condition of these fish was not good for their length and age. The length varied from 11 to 15 in., the age generally being more than three years. Expulsion of food from the front part of the stomach, an action which may take place in fish caught by a hook (Phillips quoted by Pentelow (**1**)), was not seen. Possibly this was obviated by the methods of capture, the trout being taken by nets and spears.

In order to compare the food in winter with that in the summer, the results of the examination of the stomachs of six trout killed during the month of May are included. In this case the fish were in normal condition and were caught by anglers fishing with artificial floating fly. The trout killed in the winter were collected during November to December, 1930, and November, 1932 to March, 1933; those killed in the summer, during May, 1933. The data are compiled from the food material found in the stomach only, as the varying degrees of disintegration of different organisms in the intestine rendered data obtained from that region unreliable.

III. Results of examination.

Table I records the types of food material found in the 100 stomachs examined in the winter period, and the number of cases in which each type was found. The table also includes records of the food found in the six stomachs examined during May for comparison.

Table I. *Food of 106 Trout from River Test, Hants.*

Food Material	No. of occurrences: Winter (100 trout)	Summer (6 trout)
Pisces		
Gasterosteus spp.	9	—
Gobio gobio L.	2	—
Mollusca		
Limnaea stagnalis L.	1	—
L. peregeri Müll.	10	2
Physa fontinalis L.	37	—
Planorbis spp.	8	—
Other Mollusca	4	—
Insecta		
Diptera		
Aquatic larvae	3	—
Hilara sp. imago	—	1
Coleoptera		
Aquatic larva	1	1
Trichoptera		
Rhyacophila sp. larva	2	—
Agapetus sp. larva	10	1
Agapetus sp. pupa	—	1
Sericostoma personatum Spence. larva	10	2
Silo nigricornis Pict. imago	—	1
Silo sp. larva	—	1
Halesus spp. and Stenophylax sp. larvae	17	—
Anabolia nervosa (Leach) Curt.	4	—
Other Trichoptera larvae	3	—
Neuroptera		
Sialis sp. larva	7	1
Hemiptera		
Sigara striata Fieb.	7	1
Ephemeroptera		
Baetis spp. imagines	—	3
Baetis spp. sub-imago	1	—
Baetis spp. nymphs	7	6
Crustacea		
Gammarus pulex	86	4
Asellus aquaticus L. and A. meridianus Rac.	52	—
Miscellaneous	6	—

In Table I organisms which only occurred once have been collected into groups, as far as possible. Thus, "Other Mollusca" comprise *Ancylastrum fluviatile* Müll., *Bithynia tentaculata* L., and species of *Valvata* and *Pisidium*. "Other Trichoptera" include larvae of *Odontocerum albicorne* Scop., *Silo* sp. and a Hydroptilid. The aquatic larvae of Diptera consist of *Eristalis* sp., *Dicranota* sp., and a Chironomid. The larvae of Coleoptera in both tables were not identified. The miscellaneous material comprises bread, meat refuse, and the non-aquatic organisms: *Forficula*, *Porcellio* and a Lumbricid worm.

IV. Discussion.

The occurrence of most of the food organisms observed in the stomachs is correlated with their abundance and extent of distribution in the river. The whole area, from which the trout were taken, may be divided into:

(*a*) The shallow regions, with a depth of 6–24 in., where the river bed con-

sists of stones and gravel. Here the rate of flow is comparatively high and the deposition of silt is limited to small areas enclosed by masses of aquatic plants.

(*b*) The regions with a depth of 24–50 in. and a lower rate of flow, where silt is deposited over the whole of the river bed: these regions form a minor part of the whole area.

It will be seen from Table I that *Gammarus pulex* is predominant in occurrence, and in each stomach it was found to form the bulk of the food. *Gammarus* is abundant in all parts of the river studied. In many cases, stomachs containing *Gammarus* also contained a few specimens of *Asellus*, and although the latter favours the slowly flowing, silted regions it is of sufficiently general distribution to ensure its appearance in a large number of stomachs. Of the Mollusca, *Physa fontinalis* is the most abundant and generally distributed *Limnaea pereger*, while of similar distribution is less abundant, and *Planorbis* spp., *Bithynia tentaculata*, *Valvata* sp., *Pisidium* sp., are to be found principally in the slowly flowing regions.

Seasonal abundance in the river is exemplified by the Trichoptera. The larvae of those species occurring in ten or more stomachs were more numerous than the remaining Trichopteron forms during the period to which Table I refers. Although the number of Ephemeroptera nymphs is greatly reduced during the winter, their occurrence in Table I is less than would be inferred from their numerical strength and general distribution. This contrasts with their occurrence in all the trout examined during May. The number of stomachs examined in summer is too small to be truly representative of the summer food, but it does indicate that *Gammarus* and the Trichoptera larvae still form a large part. Individually, in most stomachs the bulk of the food consisted of *Gammarus*. Food falling into the river by chance and not of aquatic derivation is of minor importance as compared with other records of the food of trout in rivers (Pentelow (**1**)) and lakes (Perkins (**2**) and Rushton (**3**)).

V. Summary.

1. The results of examination of the stomachs of 106 brown trout (*Salmo trutta* L.), from the River Test, are given, of which 100 were collected during the period from November to March and six during the month of May.

2. The predominant organisms forming the food of trout are those which are most abundant and generally distributed in the river.

3. In the material collected during the winter, nymphs of Ephemeroptera occurred to a lesser extent than would be inferred from their abundance at that period.

4. The principal difference between the winter and summer records is an increase in the number of Ephemeroptera nymphs and imagines in the latter.

VI. Acknowledgment.

The author wishes to express his thanks to Dr W. Rushton, St Thomas's Hospital Medical School, London, under the direction of whom the work has been carried out.

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(2) **Perkins, R. C. L.** (1921). "A trout's meal." J. Torquay Nat. Hist. Soc. 1921, 3.

(3) **Rushton, W.** (1921). "Biological notes." Salmon and Trout Mag. p. 63.

NOTE

WOOD ANT ENQUIRY.

I AM in search of information in connection with a survey of the distribution of the wood ant, *Formica rufa*, in the British Isles, and the Editor, to whom my thanks are due, has kindly allowed me to insert a questionnaire in this *Journal* in the hope that some of its readers may be able and willing to give assistance. *Formica rufa*, the common wood ant, is also called locally the horse, fallow, or hill ant. It occurs in woods, particularly with coniferous trees, where it builds large mound-like nests of vegetable débris (sticks, leaves, pine-needles, etc.), which may reach a height of 3 ft. or more. These nests are usually made by the side of paths, in clearings and along the edges of woods. The worker is red, with dark brown or blackish brown legs, antennae and abdomen, and the front of the head is also brown. The ant varies in length from a quarter of an inch to nearly half an inch. Answers to the following questions will be appreciated:

(1) Name and situation of wood where species occurs.
(2) Under what trees are the nests built?
(3) Nature of the soil.
(4) How many nests are there in this locality?
(5) Are the ants increasing or decreasing in number?
(6) For how many years have they been there?

I should be particularly interested in records for beechwoods and calcareous soils. Records for localities where this species has now died out would also be of value, more especially if the cause of extinction is known.

Any information, for which I shall be most grateful, should be sent to me direct at the address given below:

MISS ENID NELMES,
27 WESTBOURNE AVENUE,
ACTON,
LONDON, W.3.

REVIEWS

THE FEBRUARY ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. XXII, NO. 1).

THE current issue of the *Journal of Ecology* contains sixteen papers and notes, a letter to the Editor, some minor reviews, an announcement by the British Empire Vegetation Committee, reports of the meetings of the British Ecological Society, the annual statement of accounts, and the current list of members.

Prof. Boycott's paper on "The Habitats of Land Mollusca in Britain," an elaboration of part of his Presidential Address of 1933, may be thought to belong more properly in the *Journal of Animal Ecology*; but its wide general interest to ecologists at large has decided its inclusion in the parent *Journal*. Dr Clements contributes an important paper on "The Relict Method in Dynamic Ecology," in which he describes the tracing of successions, with the help of the presence of relicts from former stages, in a wide variety of North American formations, illustrating his account by a number of instructive photographs.

Four papers deal with tropical vegetation. Messrs Davis and Richards publish the second part of their intensive study of a small area of rain forest on Moraballi Creek, British Guiana: Mr J. D. Scott an account, notable for the large amount of instrumentally recorded habitat data, of the vegetation at Kikori (Tsetse Research Station) in the Central Province of Tanganyika Territory; and Capt. C. R. Robbins a description of an attempt at land classification in Northern Rhodesia with the help of aerial photography. This last is illustrated by some striking vertical and oblique photographs from the air. Mr E. B. Martyn contributes a short but instructive paper on the colonisation of the foreshore near Georgetown, British Guiana, by mangroves and by a tropical species of "rice-grass," *Spartina brasiliensis*.

Widely different climatic vegetational formations are represented by Mr J. G. Wood's investigations of the physiology of Australian xerophytes of different types, by Mr A. P. G. Michelmore's account of the vegetation of Edge Island and Barents Land, Spitsbergen, and by the first part of Dr A. S. Watt's study of the Chiltern beechwoods.

Mr G. H. Bates shows that curtailment of the root system of white clover, whether by direct cutting or indirectly caused by cutting or injuring the leaves, leads to the formation of smaller leaves: also that the *p*H value of the medium has a marked effect on development of the root system. Mr Wyllie Fenton traces the opposed changes in Devonshire pastures brought about by suitable grazing and manuring on the one hand, and on the other by the natural succession of neglected grassland to heath or scrub and woodland. Dr W. E. Isaac contributes a note on the "rate of decay" in different soil types of Glamorganshire, as measured by the evolution of CO_2 when the soil is mixed with a small proportion of linseed meal. Dr Dudley Stamp proposes a system of characterisation of types of vegetation by formulae, with the object of expressing, by means of symbols, certain of the most important features of a plant community in a short space, the simpler types of formulae being easily constructed by a traveller who is not an expert botanist, and at the same time ensuring that essential features are recorded. Dr Dudley Buxton contributes a short note on the willows of the western end of the Isle of Wight; and Dr M. C. Rayner a criticism of some recent publications on the mycorrhiza of forest trees, stressing the importance of observation and study of mycorrhiza first of all in natural stands of the trees concerned. Mr A. P. G. Michelmore, in a letter to the Editor, criticises the treatment of succession by some recent authors, particularly Prof. John Phillips, who will reply in the next issue of the *Journal*. The British Empire Vegetation Committee announce with regret the discontinuance of "British Empire Vegetation Abstracts" and note the progress of other sides of their work.

A. G. TANSLEY.

AFRICAN LAKES.

S. and E. B. Worthington. *Inland waters of Africa. The result of two expeditions to the Great Lakes of Kenya and Uganda, with accounts of their biology, native tribes and development.* 259 pp. (with 40 plates, 13 text-figures and one map). London, Macmillan and Co., 1933. Price 15*s*.

There have seldom been two such fruitful and interesting expeditions as those described in this book and it is very fortunate that Dr and Mrs Worthington have undertaken the task of presenting the story to a wider public than that which reads the Government Reports and scientific periodicals in which the results have, for the most part, already appeared.

The earlier chapters describe the area investigated, the geography of the Rift valleys and the general features of the various types of lake, the methods of travel and the kind of boats used by the expeditions. Then follow excellent descriptions of surveys of Lakes Rudolf, Edward, George and Bunyoni. These chapters are very attractively written and convey very clearly the conditions under which the work was carried out. The authors give a good popular account of the mammals, birds and fishes of the Great Lakes, including a topical allusion to the "Monster" of Victoria Nyanza. The aims and objects of ecology are very well described for the non-technical reader, though it might be suggested that the study of food-chains is not the only object of that branch of science.

One of the most important chapters deals with "Farming the Waters." There is in Kenya and Uganda an area of water equal to one-fifth that of the North Sea. Practically all this water is potentially productive of fish but at present the yield is very small. In a country in which famines are not unknown, such a source of food is of great importance and the improvement of the fisheries is an urgent necessity. The policy at present adopted tends towards the introduction of species of economic value into waters which were hitherto barren or contained fish unsuitable for commercial exploitation. Some of these introduced fish are African; but European and American species are also already acclimatised in some waters. Thus both *Tilapia* (African) and black bass (American) have been introduced into Lake Naivasha; and trout, both brown (European) and rainbow (American) into the mountain streams of Kenya; while the introduction of the Nile perch (African) into Lake Victoria is suggested. After a careful survey of the facts the authors give their cautious approval to this policy. They may be right; certain it is that such areas of potentially productive water cannot be left undeveloped, but whether the introduction of foreign species is altogether desirable has yet to be proved. It is suggested that by stocking Lake Victoria with Nile perch, the enormous population of *Haplochromis* which inhabits the open waters of the lake, would become available as food for the perch which would, in turn, serve as food for man. The interposition of another link into the food-chain, however, results in considerable waste and if the claims of sport be ignored, it would be more economical to develop, under proper safeguards, a trawl-fishery for *Haplochromis* itself. This chapter, and the one on trout in Kenya, deserve the careful study of all those interested in fishery problems.

The curious distribution of the fauna of these lakes is explained by the facts of the prehistory of the continent, with its alternating arid and pluvial periods, and the absence of crocodiles from Lakes Edward and George has received what is probably its final explanation from the authors. Native methods of fishing and boat-building are very clearly described and a final chapter gives a short account of some of the everyday activities of these interesting people. The plates are exceedingly good and the map is adequate, though contours would increase its interest.

F. T. K. PENTELOW.

ANIMAL ECOLOGY

Charles Elton. *The ecology of animals.* 97 pp. Methuen's Monographs on Biological Subjects, edited by G. R. de Beer. London, Methuen and Co., 1933. Price 3*s.* 6*d.*

Charles Elton. *Exploring the animal world.* 119 pp., with 3 woodcuts by Nora S. Unwin. London, George Allen and Unwin, Ltd., 1933. Price 3*s.* 6*d.*

Mr Elton's two little books are welcome evidence of the increasing popularity and importance of Animal Ecology. The first, which is the longer, though it has the smaller number of pages, belongs to Dr de Beer's excellent three-and-sixpenny series, and is intended as an elementary introduction for those who may become serious students of the subject. The chapter headings will give some idea of its scope—"The Scope of Animal Ecology," "Ecological Surveys," "Animal Inter-relations," "Habitats," "Numbers—Statistics and Dynamics," "Economic Problems." The book is packed with items of information of interest to all ecologists. One of these is the accumulating evidence that animals sometimes choose their habitats not for reasons involving survival value, but because they like them, and that they may avoid others which they dislike but which we cannot believe are in any way dangerous or biologically disadvantageous. It is a question whether such "psychological" behaviour has any relation to natural selection. Another interesting point brought out by Mr Elton is the comparatively narrow limits of variation in the number of species of animals inhabiting any given limited habitat. The fluctuations in the numbers of individuals of a given species from year to year, and the cycles of rise and fall in the size of animal populations are topics now undergoing the most rapid current development, and in which Mr Elton himself is a leading worker and authority. The ultimate causes of the cycles are still largely obscure, but the author shows clearly that the fluctuations of different species are often causally and closely interlocked.

Exploring the Animal World is based on a series of broadcast talks, and forms a most attractive introduction to the subject for the plain man. Many of the same topics are dealt with, and the whole is leavened with the author's characteristic quiet and often whimsical humour. That the material made attractive and fruitful broadcasts is shown by the fact, mentioned in the preface, that an inquiry into woodland bird life was carried out with the help of various listeners; the results will be published in the *Journal of Animal Ecology.* Miss Unwin's three woodcuts show considerable sense of decoration and certainly embellish the book; one would indeed have welcomed three times as many, especially if they had all been closely related to the situations described by the author.

A. G. Tansley.

MARINE PLANKTON: SEASONAL CYCLES.

A. G. Nicholls. *On the biology of* Calanus finmarchicus. (1) *Reproduction and seasonal distribution in the Clyde Sea Area during* 1932. (2) *Seasonal variations in the size* (by S. M. Marshall). (3) *Vertical distribution and diurnal migration.* J. Marine Biol. Ass. 19, 83–164, 1933.

These three papers contain in the main an enlargement and confirmation of the original work and suggestions of F. S. Russell at Plymouth. It is advisable as a preliminary to read Russell's paper in the *J. Marine Biol. Ass.* 15, 429–54, 1928.

The first paper contains the results of vertical hauls with a modified Standard net at fortnightly intervals at four stations in the Clyde Sea Area. The catches were sorted into 14

different categories—ova, 6 nauplius stages, 5 copepodite stages and adult male and female—and were afterwards counted. The results for station 2 in particular, confirm Russell's work in showing, with almost diagrammatic accuracy, three breeding periods in March, May, and July. Each maximum of females is followed by a maximum of ova which can be traced through each stage to the adult. The winter hauls confirm Farran's work in showing the predominance of the fifth copepodite stage at this season.

The second paper gives measurements of the cephalothorax of the adults and stages 4 and 5 of the copepodites picked out from Nicholls' catches. The results again confirm Russell's work in showing that the size was greatest in the spring, when development had taken place at minimum sea temperature, and smallest at the end of summer.

The third paper gives two sets of observations in Loch Fyne in January and July, on vertical hauls taken every three hours throughout a day, with a closing net dividing the total depth into six sections. The distribution picture shows that the ova, nauplius, and copepodite stages 1, 2, and 3, are most abundant in the upper 30 metres, whilst the later stages and adults are more generally distributed and show diurnal vertical movements.

It is to be regretted that hydrographic observations were not carried out simultaneously with the plankton collections. Temperature records would be especially useful to correlate with the size and rate of growth data, whilst routine hydrographic sections through the Arran Basin and Loch Fyne would give some clue to the water movements in these semi-enclosed areas.

Mr Nicholls is to be congratulated on maintaining such intensive routine observations throughout a year. Such data form the foundation stones of modern marine ecology. A year's observations as intensive as these on a Boreo-Arctic species such as *Calanus finmarchicus*, at its northern limit of distribution, is now badly needed.

F. C. STOTT.

THE SPREAD OF THE BLACK-NECKED GREBE.

Heinrich Frieling. *Die Ausbreitung des Schwarzhalstauchers,* Podiceps nigricollis nigricollis *Brehm. Ein Beitrag zur kausalanalytischen und vergleichenden Tiergeographie.* Zoogeographica 1, 485–550, 1933.

Asking himself the questions how and why the black-necked grebe has lately extended its range, Herr Frieling proceeds to review in some detail evidence regarding the distribution of the species in central, northern and western Europe. He next examines the areas newly colonised, the dates of colonisation, the directions of expansion, the mechanical limits to expansion, the pattern of the expansion, the relation of the black-necked to other grebes, from an ecological and distributional standpoint, and the effect of the ice age in stimulating the expansion of the species. Obviously Herr Frieling is a courageous man. Those who have some experience of the obstacles which handicap collection of accurate and full data on subjects of this nature even for so compact and comparatively well observed an area as England and Wales will watch with fascination the manner in which he skims lightly from one part of Europe to another, listing in turn colonies breeding alongside blackheaded gulls in Prussia, colonies springing up on newly-made ponds in Bavaria, colonies in Denmark, Ireland, Czechoslovakia and so forth. Unfortunately this ambitious scope has made it impossible for the writer to undertake an original investigation commensurate with the scale of his subject; he has had to content himself with what published and unpublished material he could find, mostly in smallish fragments. How faulty such a foundation may prove for far-reaching generalisations is amply demonstrated by the treatment of British evidence. Citing two different authorities, Herr Frieling remarks that there are recently colonised breeding places in Oxfordshire and Norfolk, that the species probably also breeds in Oxon. and Perth, and that the best-known English breeding places are in Wales and at Tring reservoirs. Turning

to Scotland he refers to a breeding locality in the Forth region. It may be unreasonable to expect a foreigner to know that Oxon. is an abbreviation for Oxfordshire, that Wales is not in England, and that Perth is in Scotland close to the Scottish locality dealt with under a separate heading; but surely any British ornithologist who had been shown the MS. could have set the writer right on this at once. The present reviewer took up this paper eagerly in the hope that it might throw some light on the highly obscure situation of this species in Ireland, where it was first found nesting within the last twenty years, and where a colony of as many as 250 nests has lately been discovered. It was astonishing to find that Herr Frieling has taken this fragmentary information and on the strength of it drawn a curve like the side of a house depicting an increase from 1 pair in 1915 to 250 pairs in 1930. Examination of the available accounts (for instance *British Birds*, 24, 170–5, which is referred to by the writer under two misspelt names and which is at variance with his narrative on material points) will show that the sweeping conclusions of sudden invasion based largely on this Irish example must be utterly worthless. We simply do not know how long the black-necked grebe has bred in Ireland, nor in how many localities, nor is there any material for suggesting a centre of dispersal. There are probably not a dozen people in Ireland who would know a black-necked grebe if they saw one. We do know that the actual curve drawn by Herr Frieling is completely out, because the large colony in question has now been ascertained to have existed at any rate some years before the "discovery" reported. So in fact has the Welsh colony of which he writes "wo plötzlich 1904 5 P. erstmalig auftraten": the *British Birds* account above cited says "there is evidence to show that the birds were in this district twelve years prior to 1904." Curiously enough the one recent English example of an apparently sudden colonisation by several breeding pairs in Yorkshire in 1928 (*British Birds*, 24, 222) is never mentioned by Herr Frieling, who remarks with his inimitable aptitude for misleading generalisation, "Überhaupt scheint in England keine Neigung zu Invasionswiederholungen bis jetzt bestanden zu haben."

Herr Frieling puts forward some theories which are interesting but which remain to be substantiated. In concentrating on his shortcomings we must not overlook the fact that he has done a stimulating piece of work which it may in fifty years time be possible to carry out satisfactorily. At present there is little to be gained by leaping ahead of the facts.

E. M. NICHOLSON.

JACK RABBITS AND GRAZING PROBLEMS.

Charles T. Vorhies and Walter P. Taylor. *The life history and ecology of Jack rabbits*, Lepus alleni *and* Lepus Californicus *spp. in relation to grazing in Arizona.* University of Arizona College of Agriculture, Technical Bulletin No. 49, 1–117, 1933.

The work on which this publication is based has been carried on separately and together by the two authors over a period of about 15 years. Of the two species of jack rabbits which have been studied *Lepus alleni* has a limited distribution in Arizona, *Lepus californicus* being generally distributed throughout. Particular attention has been given to the food of the two species and the effects of rabbit grazing on the cultivated crops, range pasture, and forests. Field observations are supported by convincing quantitative data obtained from quadrat experiments and stomach examinations. Figures have been obtained for the weight of food eaten by rabbits and interesting quantitative comparisons are possible between sheep, cattle and rabbit grazing. Normally, over large areas, the jack rabbits do not appear to have a very serious influence on the grazing of cattle ranges. In the area studied the rabbit population was estimated to be about 7 per cent. by weight of the cattle stock and to eat about 5 per cent. of the valuable grazing; but locally and at different times the economic influence may be much greater than this.

Much valuable work has been done on census methods, parasites, predators, habits, reproduction and methods of rabbit control, but its importance does not end merely in more knowledge of jack rabbits in Arizona. Field investigations of this nature, centred on the ecology of one particular animal, are of great value to animal ecology, since they not only provide facts but evolve accurate methods for census work and recording observations in a systematic manner. In more and more aspects of animal ecology scientific conclusions can only be reached when the field data are recorded in such a way that they can be subjected to statistical treatment.

A. D. MIDDLETON.

ECOLOGY IN GAME CONSERVATION.

Aldo Leopold. *Game management.* 481 pp. New York, Charles Scribner's Sons. 1933. Price 21*s*.

THE ecology of American game populations has been receiving a good deal of serious study recently. Hitherto, American sportsmen have done little to conserve their game except shoot it or refrain from shooting it, but it is safe to say that during the last ten years every sensible sportsman in America has realised that he cannot have game to hunt unless he takes care that a suitable environment is maintained for the game species to live in. Game conservation means conservation of the optimum environments for the various species: this is applied ecology. Scientists like Leopold and Stoddard are among the limited numbers of workers who are carrying out scientific studies of animal ecology with a view to the immediate application of ecological knowledge to the control of animal populations.

About a third of the book is taken up with a careful analysis of the ecological principles and factors concerned in the natural control and maintenance of wild game populations, while the remainder is devoted to more detailed discussions and examples of the application of these principles to conservation and management. About thirty species of game animals are treated and, since they range from quail and rabbits to sea ducks and grizzly bears, Leopold's work is concerned more with general principles of population control than with detailed studies of particular species. The bob-white quail (which is really a partridge) has received more attention than most of the other species, as it is an important game bird which is susceptible to environmental control. Stoddard's extensive studies of quail in Georgia[1] have furnished more abundant data on this species than are available for any other game bird. Apart from the directly acting "simple" environmental factors, Leopold emphasises the facts and importance of cyclic or periodic fluctuations associated with disease. The available data on this subject are admittedly inadequate for any real conclusions as to the nature and causes of the fluctuations in numbers of American game species, but there can be no doubt of their importance in a long-term conservation programme.

To ecologists one of the most important features of the book is the clear statement of the idea of interspersion of habitat types in the optimum environment for any species of low mobility: Population density is largely determined by an optimum "mixing" of food, shelter, nesting cover and other factors over an area determined by the "cruising radius" of the species. It should be possible to describe the optimum environment for a species by a formula based on more adequate knowledge of this Law of Interspersion. Successful management of game bird populations such as quail, grouse and partridge certainly depends largely on a proper understanding of this law and the underlying ecological principles. The book furnishes a good example of the possibility of rapid and economic application of ecology to population control of both mammals and birds and as such is of paramount interest to both ecologists and conservationists.

A. D. MIDDLETON.

[1] **H. L. Stoddard,** *The Bobwhite Quail, its habits, preservation and increase,* New York, 1932.

Malcolm Stewart. *Ronay: a description of the Islands of North Rona and Sula Sgeir, together with their geography, topography, history, and natural history, etc., to which is appended a short account of the Seven Hunters, or Flannan Islands.* 73 pp. with 4 maps. Oxford University Press, 1933. Price 7*s.* 6*d.*

THE title of this book fully describes its general scope, but it should be clearly realised that the work is much more than an ordinary guide to the islands and represents a considerable amount of search into maps and records, as well as personal expeditions to islands which are not easy to reach. It is interesting to know that, in spite of its relative inaccessibility, North Rona is rented by a sheep farmer from Lewis, who visits his flock every year. Among other subjects, the natural history of the islands is summarised so far as it is known, and there are a number of photographs.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

Note. Entomological journals have been abstracted by H. F. Barnes and B. M. Hobby, forestry journals by D. H. S. Davis.

Copies of these abstracts, cut down to a width suitable for pasting on to five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 200 notices, in two sets, May and November).

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

1. Collin, J. E. (1933). "Five new species of Diptera." Ent. Mo. Mag. 69, 272–5.

Contains records of flies reared from birds' nests.

2. ECOLOGICAL SURVEYS AND HABITAT GROUPS.

(*a*) Marine.

See also **10, 23.**

2. Palmer, R. (1933). "Notes on *Gammarus zaddachi* Sexton from Essex, with observations on eye-variations in this species." Ann. and Mag. Nat. Hist. 11, 64–7.

Notes on occurrence of this race or species in brackish water.

3. Crossland, C. (1933). "Distribution of the Polychaete worm, *Syllis ramosa* McIntosh." Nature, 131, 242.

This remarkable branching marine worm is now recorded from shallow water by the Marine Biological Station at Ghardaqa in the Red Sea.

(*b*) Freshwater.

See also **23, 30, 99.**

4. Macan, T. T. (1933). "An inland record for *Theobaldia* (*Culicella*) *litorea* Marshall and Staley (Diptera, Culicidae)." Entomologist, 66, 260–1.

A mosquito.

5. Marshall, J. F. and **Staley, J. (1933).** "A new British record of *Orthopodomyia pulchripalpis* Rondani (Diptera, Culicidae)." Nature, 131, 435.

A rare tree-hole species of mosquito.

6. Van Someren, V. D. (1933). "A Scottish occurrence of *Craspedacusta sowerbii* Lankester." Nature, 132, 315.

The medusoid phase found in freshwater tropical aquarium near Edinburgh. Previously known in this country from botanic gardens, and occurring wild in China, U.S.A. and Panama.

7. Tattersall, W. M. (1933). "Occurrence of *Craspedacusta sowerbii* Lankester, in Monmouthshire." Nature, 132, 570.

Medusae found in a reservoir, apparently not warm water.

(*c*) Land.

See also **1, 44, 52.**

8. Lancashire and Cheshire Fauna Committee (1933). "Nineteenth annual report, and report of the recorders for 1932." (Published by T. Buncle and Co., Market Place, Arbroath.) Address of Secretary: 11 Addison Road, Hale, Cheshire.

This report contains lists of animals, edited by various authors, mainly referring to localities and dates of record, but also including a good deal of useful data about habitats. The following

sections are of interest to ecologists: *Vertebrates* for Cheshire and South Lancashire (**A. W. Boyd**), mainly bird notes, together with some on squirrels; *Birds* in North Lancashire (**H. W. Robinson**); *Sawflies* (**H. W. Miles**) with habitat notes; *Arachnida* (**A. R. Jackson, W. Falconer**), includes spider apparently introduced into Britain, a number of habitat notes for spiders (many from sand dunes), etc.; *Plant galls* (**W. Falconer**); a valuable list of *Bird-lice* (**H. Britten**) from named hosts, and in the same section *Lice* and *Fleas* from mammals, and *Beetles, Flies, Parasitic Hymenoptera,* and introduced *Orthoptera.*

9. Fox Wilson, G. (1933). "Contributions from the Wisley Laboratory, 65: Pollination in orchards (8)." J. Roy. Hortic. Soc. 58, 125–38.

A full account with tables showing species of insects visiting various fruit trees and bushes, and notes on effects of different conditions upon insect visitors.

10. Renouf, L. P. (1933). "Some air-breathing arthropods of the littoral region of the coast of County Cork, I.F.S." Ann. and Mag. Nat. Hist. 10, 262–7.

11. Donisthorpe, H. (1933). "Additional records of ants and myrmecophiles in Britain since the 2nd edition of *British Ants* (1927) and my paper on the ants and myrmecophiles of Windsor Forest (1930)." Ent. Rec. 45, 132–6.

Contains numerous new distributional and habitat records, etc.

12. Niblett, M. (1933). "British gall-causing Cynipidae: some notes on their emergences." Entomologist, 66, 149–53.

13. Petherbridge, F. R., Thomas, I. and **Hey, G. L. (1933).** "On the biology of the plum sawfly, *Hoplocampa flava* L., with notes on control experiments." Ann. Appl. Biol. 20, 429–38.

Includes notes on variation in susceptibility of plum varieties to attack. Further reference in **H. W. Miles, I. Thomas** and **G. L. Hey,** ibid. 722–30.

14. Thomas, I. (1933). "On the bionomics and structure of some Dipterous larvae infesting cereals and grasses. I. *Opomyza florum* Fabr." Ann. Appl. Biol. 20, 707–21.

The wheat variety Old Fashioned II was found to be more resistant to attack than other varieties.

15. Barnes, H. F. (1933). "A cambium miner of basket willows (Agromyzidae) and its inquiline gall midge (Cecidomyidae)." Ann. Appl. Biol. 20, 498–519.

Résumé of information about Dipterous cambium miners (Agromyzidae). Morphology and bionomics of *Dizygomyza barnesi* Hendel sp.n. are described. List of *Salix* species attacked by the larvae is given, as well as records of two Braconid parasites and an inquiline gall midge and its parasites.

16. Lal, K. B. (1933). "Biological races in *Psyllia mali* Schmidberger." Nature, 132, 934.

This apple-sucking bug lives also on hawthorn in Scotland, and forms a phenotypic variety on that plant. This variety is attacked by certain parasites from which the apple race is free.

17. Donisthorpe, H. (1933). "The true habitat of *Gyrophaena lucidula* Er., and *G. convexicollis* Joy." Ent. Rec. 45, 126–7.

Found in the fungus *Lentinus trigrinus* at the roots of willows in a willow-swamp.

18. Donisthorpe, H. (1933). "Further notes on a willow swamp in Windsor Forest." Ent. Rec. 45, 4–5.

218 species of Coleoptera have been recorded from this one small area.

19. Hey, G. L. and **Thomas, I. (1933).** "On the biology of *Cacoecia crataegana* Hüb. (Lepidoptera: Tortricidae) on fruit trees in the Wisbech area." Ann. Appl. Biol. 20, 439–62.

Account of life history, habits (including egg-laying), and parasitism of this moth.

20. Bristowe, W. S. (1933). "Notes on the biology of spiders. 10: British cellar spiders, with the description of a species new to Britain." Ann. and Mag. Nat. Hist. 11, 509–14.

Contains lists of spiders found in seven different cellars in the south of England, and a few notes on animals associated with them.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **9, 56, 57.**

21. Lack, D. (1933). "Nesting conditions as a factor controlling breeding time in birds." Proc. Zool. Soc. London, 231–7.

An ecological factor, the date at which nesting sites become available—is very important in determining the onset of egg-laying in birds, and cuts across climatic factors, such as light and temperature influencing the state of the gonads. This hypothesis is illustrated by data for the Arctic Tern on Bear Island and also for other birds in various parts of the world. Variable dates of nesting site availability in different years may be one cause of fluctuations in bird populations.

22. Lack, D. and **L. (1933).** "Territory reviewed." British Birds, 27, 179–99.

An important discussion of Howard's territory theory and the concept of food as limiting factor in bird territory. The authors believe that territories are determined mainly by the psychological peculiarities of the birds, and have no adaptive relation to food supply.

23. Water Pollution Research Board (1933). "Report for the year ended 30th June, 1933." Dept. of Scientific and Industrial Research. (H.M. Stationery Office, Price 1*s*.)

In addition to a great deal of information about effluents and results of studying them, there is special interest to ecologists in the summarised account of a large scale survey of the River Tees in relation to pollution. Both chemical and ecological work was done at a number of stations. The full lists of animals and plants from various habitats remain still to be published. The Tees shows a gradient from non-tidal to tidal, and the non-tidal is again divided into an upper section of soft water and a lower section with double the hardness. There is also a gradient of increasing sewage. The non-tidal is not sufficiently polluted to harm trout, in fact the effect of moderate sewage pollution is to increase the plant and animal life. The limits of various species are indicated, with special reference to certain algae, insects, and molluscs. Seasonal fluctuations were also studied. Owing mainly to effects of cyanide pollution from factories the tidal estuarine region forms a serious barrier to migrating fish, of which many are killed. The central estuarine region is also barren in other animal life, but this is shown to occur also naturally in the non-polluted Tay and Tamar.

24. Mellanby, K. (1933). "The temperature of the insect's environment." Proc. R. Ent. Soc. London, 8, 22–4.

The temperature among grass, in rat holes, moist soil, etc. may be several degrees lower than that of the air immediately above, owing to the evaporation of water. In such situations very steep temperature gradients exist, and when an insect appears to be attracted by moisture or some chemical stimulus, it may actually be attracted by a low temperature. Whenever possible, the conditions at the *exact* spot where the insect is resting should be measured, for they may be quite different from those even a few inches away.

25. Gunn, D. L. (1933). "The temperature and humidity relations of the cockroach (*Blatta orientalis*)." J. Exp. Biol. 10, 274–85.

26. Jackson, Dorothy J. (1933). "Observations on the flight muscles of *Sitona* weevils." Ann. Appl. Biol. 20, 731–70.

Breeding evidence of *S. hispidula* shows that unfavourable conditions during development may be responsible for the production of the flightless weevils.

27. Smith, P. S. (1933). "Hibernating insects." Ent. Rec. 45, 26–7.

Records hibernation of *Cidaria miata*, *Scoliopteryx libatrix*, *Polygonia c-album* and *Vanessa urticae* (Lep.). Also queen wasps and a green lacewing.

28. McAtee, W. L. (1933). "Rejoinder to papers on Protective Adaptations recently published by the Entomological Society of London." Proc. R. Ent. Soc. London, 8, 113–26.

"My opponents believe that protective adaptations have an important influence on predation which is therefore discriminate, while I believe that predation is largely controlled by numerical factors and tends to be indiscriminate."

29. Simons, L. (1933). "The international phenological journal, *Acta Phaenologica*." Nature, 132, 172.

A new journal (published in Holland), which has had financial difficulties at the start, but aims at coordinating phenological records.

30. Boycott, A. E. (1933). "The pearl mussel (*Margaritina margaritifera*) in hard and soft water." Vasculum, 19, 47–51.

Although generally thought to be restricted to soft waters (hardness—in milligrams of calcium per 250 c.c.—less than 30), it has occurred in rivers with hardness up to 79. Figures for the calcium content of a number of rivers are given, and relations to factors affecting the pearl mussel discussed.

31. Beauchamp, R. S. A. (1933). "Rheotaxis in *Planaria alpina*." J. Exp. Biol. 10, 113–29.

This planarian worm is normally negatively rheotactic and moves down stream. It is shown by experiment and field observation that with sexual development the worms reverse their movements and go upstream. This takes place especially in winter since sexual development takes place at temperatures below 10° C. Migration causes partial starvation through overcrowding upstream. The integration of these factors determines the distribution of *P. alpina* in upland streams.

32. Pearsall, W. H. and **Ullyott, P. (1933).** "Light penetration into freshwater. 1: A thermionic potentiometer for measuring light intensity with photo-electric cells." J. Exp. Biol. 10, 293–305.

An important contribution to methods of estimating quantity and quality of light in lakes at different depths. Two later parts (J. Exp. Biol. 10, 306–12, 1933, and 11, 89–93, 1934), discuss the relation of light conditions to plant life in Windermere. It is shown that depth of rooted vegetation depends on light and the latter to a large degree on the amount of phytoplankton.

33. Beauchamp, R. S. A. (1932). "A new dredge." Internat. Rev. der ges. Hydrobiol. u. Hydrograph. 27, 467–9.

A strong tow-net, with adjustable opening, fixed to metal runners. This can be adapted to different types of bottom.

4. PARASITES OF ANIMALS.

See also **8, 95.**

34. Richards, O. W. (1933). "Hymenopterous parasites of adult beetles." Proc. R. Ent. Soc. London, 8, 135.

There are a number of Tachinids and Braconids which are habitually parasites of adult beetles. The Braconid genus *Perilitus* contains some of the best known examples. *P. aethiops* may emerge from either larvae or adults of *Phyllotreta nemorum*.

35. Morley, C. (1933). "Notes on Braconidae: XIV. Alysiides." Entomologist, 66, 201–3.

This concludes a series of useful notes and gives a list of the hosts, inquilines, etc.

36. Edelsten, H. M. (1933). "A Tachinid emerging from an adult moth." Proc. R. Ent. Soc. London, 8, 131.

In this communication several instances of parasites emerging from the bodies of *adult* Lepidoptera are recorded.

37. Taylor, J. N. (1933). "Mermithogynes." Ent. Rec. 45, 162–4.

A nest of *Acanthomyops flavus* contained numerous individuals parasitised by Nematode worms (56 parasitised females and 13 parasitised males being obtained in two visits to the nest). Neighbouring nests of *A. niger* and *A. flavus* were unaffected.

38. Lapage, G. (1933). "Cultivation of parasitic nematodes." Nature, 131, 583–4.

Gives methods of culturing parasitic nematodes from mammals such as the sheep and rabbit, in order to obtain larval stages.

39. Jepps, M. W. (1933). "Miracidia of the liver fluke for laboratory work." Nature, 132, 171.

40. Brown, F. J. (1933). "Life-history of the fowl tapeworm, *Davainea proglottina*." Nature, 131, 276–7.

The slug *Agriolimax agrestis* now definitely proved to be an intermediate host of this tapeworm in Britain (as well as on Continent). The technique of keeping and infecting the slugs is described.

41. Todd, C. (1933). "The presence of bacteriophage for *B. salmonicida* in river waters." Nature, 131, 360.

The bacterium causing furuncolosis, a severe epidemic disease of salmon and trout, does not survive long free-living in river waters, but this newly discovered bacteriophage does, and may therefore become an important indicator of the presence of the disease. It was found in the Thames, Mole, Arun, Sussex Ouse, and Avon at Bath.

5. FOOD-HABITS.

See also **88.**

42. Raymond Philipson, W. (1933). "The rook roosts of South Northumberland and the boundaries between their feeding territories." British Birds, 27, 66–71.

Contains a map showing five main roosts on an area of some 1000 square miles, and boundaries between some of them. Subsidiary roosts form at the edge of the feeding areas. It is suggested that winter roost areas are also summer feeding territories.

43. Dewar, J. M. (1933). "Northumberland rook roosts." British Birds, 27, 103–4.

A note on the area mentioned in No. **42**, for the years 1904–05. The distribution of roosts was in the main much the same. On p. 140, this note is discussed by **Raymond Philipson.**

44. Armitage, J. (1933). "The association of birds and a moor-grass on the Pennines in winter." British Birds, 27, 153–7.

Molinia grass moor on the high Pennines has often a denser winter bird population than other types such as cotton grass, heather, bracken, or bilberry. This is attributed to enormous numbers of a Cecidomyid gall-midge (*Mayetiola* [*Oligotrophus*] *ventricola*) which has larvae in stems of *Molinia*. These are eaten by many birds, *e.g.* snow-bunting, reed-bunting, skylark, chaffinch, starling, partridge, magpie, etc.

45. Parkinson Curtis, W. (1933). "The Robin (*Erithacus rubecula melophilus* Hartert) destroying *Leucoptera laburnella* Stt. and *Gracilaria syringella* Fab." Entomologist, 66, 165.

These are moths.

46. Evans, C. I. (1933). "Larder of red-backed shrike." British Birds, 27, 134–5.

Contained twenty bumble bees (? *Bombus terrestris*).

47. Carpenter, G. D. Hale (1933). "Winged ants as food for gulls." Proc. R. Ent. Soc. London, 8, 111.

Mature and young Herring Gulls feeding extensively on the winged adults of the ant *Acanthomyops flavus*.

48. Oldham, C. (1933). "Gulls feeding on beetles." British Birds, 27, 169–70.

Many birds, especially gulls, eating chafers (*Phyllopertha horticola*) in Co. Mayo. Also *Rhizotrogus solstitialis* eaten by black-headed gulls in Cumberland, and ghost moth (*Hepialus humuli*) eaten by gulls.

49. Welch, F. D. (1933). "Moths attacked by birds." Entomologist, 66, 165.

50. Ticehurst, C. B. (1933). "Food of the swift." Ibis, 3, 786–7.

Full identification of insects in one stomach.

51. Tracy, N. (1933). "Pine-cone diet of great spotted woodpecker." British Birds, 26, 257–8.

Pine-cone seeds are eaten from the end of July to the following April, the birds going for green cones. The green and lesser spotted woodpeckers are mainly insectivorous.

52. Harris, G. T. (1933). "Food of the adder." Nature, 132, 482.

Records an adder hunting in a tree, and grass snake hunting under water, and gives notes on local abundance of snakes possibly correlated with geological formation.

53. Anon. (1934). "The food of young perch." Game and Gun and the Angler's Monthly, February.

A contribution from the Windermere laboratory showing the proportions of different kinds of plankton Crustacea eaten by perch of different sizes. Fish over five and a half inches do not eat plankton at all, partly owing to habit formed during the winter diminution of plankton.

54. Fryer, J. C. F. (1933). "*Phlyctenia fulvalis* and *Crambus contaminellus* in Southern England." Entomologist, 66, 265–7.

Notes on the life history and food habits of these moths.

55. Lowndes, A. G. (1933). "The feeding mechanism of *Chirocephalus diaphanus* Prévost, the fairy shrimp." Proc. Zool. Soc. London, 1093–1118.

The fairy shrimp was proved to feed on detritus, and the exact mechanism of feeding was studied by various methods, including the polygraphic process, an adaption of cinematography which gives the effect of slow motion film.

6. ANIMAL POPULATIONS.

See also **21, 22, 41, 42, 43, 52.**

56. Van Rest, E. D. and **Parkin, E. A. (1933).** "Poisson series and biological data." Nature, 132, 445.

Discusses a special statistical method of arranging the data about egg-laying frequency of powder post beetles, *Lyctus*.

57. Allee, W. C. (1934). "Recent studies in mass physiology." Biol. Rev. 9, 1–48.

An extension, with large list of references, of the author's book on "Animal Aggregations," with fresh evidence that undercrowding lowers rates of population increase in some forms. Crowding also affects rates of learning of higher animals.

58. Peskett, G. L. (1933). "Growth factors of lower organisms." Biol. Rev. 8, 1–45.

Full summary, with bibliography, of effects of environmental factors on population growth in yeasts, bacteria, etc., with special reference to the evidence for growth-promoting substances.

59. Parnell, I. W. and **Cameron, T. W. M.** (**1933**). "Some observations on the ecology of Scottish herbivores and carnivores." Scottish Nat.

Notes collected in course of a large scale survey of Scottish mammal parasites. Red deer increasing and spreading. Fallow and roe deer changing little. Japanese deer established at two places. Wild goats occur. Notes on distribution of badger (now introduced in north Sutherland), fox (severe mange epidemic in recent years), wild cat (spreading), polecat (nearly extinct), marten (holding its own in some districts), etc.

60. Hardy, E. (**1934**). "The black rat (*Mus rattus rattus*) on Merseyside; evidence that there is no plague danger." Naturalist, 2–3.

Statistical evidence that black rats have decreased greatly in the port of Liverpool. The number per ship has been reduced by compulsory fumigation from about 59 in 1923 to about 2 in 1932. There is no evidence that black rats are spreading inland at the expense of the brown. These figures, although only comparative and not based on censuses except in the case of ships, are decisive evidence against recent theories about the increase of plague-carrying rats.

61. Potts, G. and **others** (**1933**). Caradoc and Severn Valley Field Club, Record of Bare Facts for the Year 1932, No. 42, 7.

Many moles found dead in June above ground, uninjured.

62. Sparrow, A. H. (**1932**). Caradoc and Severn Valley Field Club, Record of Bare Facts for the Year 1931, No. 41, 7.

Half a dozen red squirrels found dead in Stretton district in 1931.

63. Harrisson, T. H. and **Hurrell, H. G.** (**1933**). "Numerical fluctuations of the great black-backed gull (*Larus marinus* Linn.) in England and Wales." Proc. Zool. Soc. London, 191–209.

A detailed study of changes in numbers and distribution. Great decrease took place during the second half of the nineteenth century, followed by increase during the last twenty-eight years. The Scilly Islands account for a large part of the present population, but Anglesey and North Wales form another important centre. The causes of the fluctuation are not clear, not being obviously associated with change in food supplies or protection. The number of breeding pairs in Britain in 1930 was estimated to be 1000–1200. The effects of the gulls on other species are noted.

64. Oldham, C. (**1933**). "Great and lesser black-backed gulls in North Wales." British Birds, 38–41.

Discusses the theory of Harrisson and Hurrell (see above) that recolonisation of Pembrokeshire by gulls took place from Anglesey as a centre. It is much more likely that it took place from south-east Ireland, *e.g.* from Saltee Islands. Criticism is also levelled at faulty facts and misquotations, leading to unreliable conclusions.

65. Morrey Salmon, H. and **Lockley, R. M.** (**1933**). "The Grassholm gannets: a survey and a census." British Birds, 27, 142–52.

An important census based on photographs independently taken and checked by two observers, with an average difference of 3 per cent. in results. Population (on island of 22 acres) was about 11,000 birds in 1933, including 1500 non-breeding birds. Up to 1914 there were less than 600 breeding birds. By 1922 there were about 3000, and in 1924 about 4000. The greatest increase was 1922–4, probably due in part to immigration, possibly from an Irish colony.

66. Robinson, H. W. (**1933**). "Great mortality among young terns in Lancashire." British Birds, 27, 138–9.

Death caused by exposure to sun resulting from visitors driving away parents. Sandwich tern colony wiped out in one place by gulls. It apparently moved to a new station farther north on the coast.

67. Roebuck, A. (**1933**). "A survey of the rooks in the Midlands." British Birds, 27, 4–23.

The survey was made in 1928. A census made in 1928–30, covering Nottinghamshire, Leicester, Rutland, Derbyshire, and parts of Lincolnshire—an area of 5305 square miles. The results are given for different unit areas, with notes on the area above 1000 feet, number of rookeries and of

nests occupied, the area under crops and grass, etc. Average for the whole area was 1 rook to every 23 acres, and therefore rather low density. Rooks nest as high as 1400 feet. There are many notes on habits, nature of rookeries, etc.

68. Harrisson, T. H. and **Hollom, P. A. D.** (**1933**). "The great crested grebe enquiry (1931). Scotland." British Birds, 26, 286–91.

Contains incomplete but detailed records for Scotland (cf. census on 69 out of probable total of 107 sites, 40 being found occupied). On the areas studied there were from 150 to 200 birds. Some evidence that the great crested grebe and the little grebe do not occur on the same waters.

69. Boyd, A. W. (**1933**). "Notes on the swallow and size of broods in Cheshire." British Birds, 26, 255–6.

A census of swallows on 2700 acres in Cheshire gave 1 swallow to every 12 acres; each farm had at least one pair. Ringing 5 birds proved that there was a high degree of local return after migration. A table shows the size of broods in 1932 (average 4·01), which was slightly greater than in 1931.

70. Stuart Bruce, R. (**1933**). "Some notes on birds seen in Shetland." Scottish Nat. 147–52.

Includes notes on recent increase of fulmar petrel (driving away herring gulls) and great skua (through protection).

71. Thursby-Pelham, D. E. (**1932**). "Report on the English plaice investigations during the years 1926 to 1930." Ministry of Agr. and Fish., Fish. Invest. Ser. 2, 12, No. 5, 1–149. (H.M. Stationery Office, price 6*s*. 6*d*., postage extra.)

An important survey of the changes in the plaice fishing industry of the North Sea. Plaice were extremely numerous and large just after the War, but gradually became reduced in the direction of danger-point already noted before the War. Restrictive legislation was proposed but not undertaken owing to resistance of the British trawling industry. At present the total catch is rising and the average size of fish declining. These changes are complicated by variations in fishing methods by which statistics are obtained, and by natural fluctuations (*e.g.* good brood years 1920–2, 1925, and 1927 and 1928, and bad ones in 1923–4, and 1926).

72. Buchanan-Wollaston, H. J. (**1933**). "Inshore trawl fisheries of Dorset and Devon. Report on researches carried out between 1924 and 1929 from Poole, Dorset, and Beer, Devon, with recommendations bearing on protective legislation." Ministry Agr. and Fish., Fish. Invest. Ser. 2, 13, No. 1, 1–69. (H.M. Stationery Office, price 3*s*. 6*d*., postage extra.)

Generally agreed that some protection is required to stop overfishing. Transportation of young plaice from Dutch grounds to Poole Harbour was not successful because the fish swam out of the Harbour and also grew more slowly than the local ones. It is thought that suitable alteration of the mesh of nets used would protect young fish to some extent and still yield high total weights of larger ones. The report is interestingly written and based on careful measurements and other observations.

73. Hickling, C. F. (**1933**). "The natural history of the hake. Part 4: Age determination and the growth-rate." Ministry Agr. and Fish., Fish. Invest. Ser. 2, 13, No. 2, 1–120. (H.M. Stationery Office, price 5*s*. 6*d*., postage extra.)

Based mainly on study of otoliths, which show annual rings and also a close relation to the size of the fish. Although hake begin to be worth selling at a length of about 13 inches (four years old), hake trawlers catch many of three years old. Herring trawlers catch large numbers of smaller hake and these were estimated on one ground to amount to a loss to the hake fishery of a million in two months, or one year's catch for two hake trawlers.

74. Wimpenny, R. S. (**1933**). "Variations in North Sea plankton, 1923–4." Ministry Agr. and Fish., Fish. Invest. Ser. 2, 13, No. 3, 1–47. (H.M. Stationery Office, price 2*s*. 6*d*., postage extra.)

The plankton was studied by several transects between England and Norway. It is suggested that certain northern species increased in 1923; this was a good survival year for haddock, which

has a northern range. Among other points discussed are: relation of diatom abundance to marine banks, seasonal succession of fat-storing and carbohydrate-storing forms, local concentration of different forms, etc.

75. Wye Board of Conservators (1933). Annual Report, Season 1933.

An analysis of the year's catches, showing relation to other rivers and to previous years, the effects of the dry summer on spawning (causing great concentration of salmon in the main river), a rather mysterious run of salmon late in the spawning season, etc. There was an extremely good run of smolts, making possible though not certain, a good crop of fish in future.

76. Barnes, H. F. (1933). "Two further instances of flies swarming at Rothamsted Experimental Station, with some references to this phenomenon." Ent. Mo. Mag., 69, 230–2.

Includes statement of the proportion of the sexes in a swarm of *Chloropisca circumdata* and *Madiza glabra* together with the Hymenopteron *Stenomalus muscarum* and also in a swarm of *Musca autumnalis* (=*corvina*).

77. King, L. A. L. and **Meikle, A. A. (1933).** "A fly pest of Timothy grass." Nature, 131, 837.

Partial stripping of flower-heads caused by a Cordylurid Dipteron, *Amaurosoma armillata*, near Stirling.

78. Mansbridge, G. H. (1933). "The breeding of *Ephestia kuhniella* Zl. in large numbers for experimental work." Ann. Appl. Biol. 20, 771–4.

79. Orton, J. H. (1933). "Summer mortality of cockles on some Lancashire and Cheshire Dee beds in 1933." Nature, 132, 314–5.

Notes on seasonal spawning periods of *Cardium edule*, and mortality of adults after spawning, due to causes unknown.

80. Stephenson, T. A. (1933). "Lunar periodicity in reproduction." Nature, 131, 622.

Production of planulae by coral *Pocillopora bulbosa* on Low Isles coral reef off Australia, shows cyclic appearance correlated with tidal behaviour.

81. Orton, J. H. (1933). "Observations of *Arenicola marina*." Nature, 132, 409–10.

Large numbers of lugworms found outside their burrows on sands of the Dee at low tide. Infection through some disease organism is suggested as cause of this unusual migration.

7. MIGRATION AND DISPERSAL.

See also **63, 64, 65, 69.**

82. Witherby, H. F. (1933). "The 'British Birds' marking scheme." British Birds, 26, 295–300.

An impressive record of patient work by a large number of observers, the results of which appear in "British Birds." In 1932, 22,950 nestlings were ringed, and 7634 birds trapped. There has been a great development of trap-ringing. Tables show the number of each species handled since 1909, and the percentage of recoveries. Notes on the use of special coloured rings are given.

83. Witherby, H. F. and **Leach, E. P.** (1933). "Movements of ringed birds from abroad to the British Isles and from the British Isles abroad." British Birds, 26, 352–61.

This valuable synthesis enables the exact records of ringing and recovery to be followed in both directions.

84. Thomas, J. F. (1933). "Some results of ringing and trapping swallows in Carmarthenshire." British Birds, 26, 253–5.

Ringing showed that out of 744 nestling swallows about 1·5 per cent. of those that were caught again had returned to the same locality to nest, the nearest being half a mile from its birthplace.

Adults ringed showed a high degree of return to the same place as previous year, often to the same shed. (See also **69.**)

85. Witherby, H. F. (1933). "Immigration of waxwings." British Birds, 26, 259, 277–8, and 313.

86. Philipson, W. R. (1933). "Notes on the migration of duck at Gosforth Park Lake." Vasculum, 19, 129–30.

Notes on abundance of various species from 1927 to 1932.

87. Russell, F. S. (1933). "Tunny in the North Sea." Nature, 132, 786.

Migration of tunny into North Sea waters not an entirely recent occurrence, since there are a number of pre-War and nineteenth century records. References given.

88. Pentelow, F. T. K., Southgate, B. A. and **Bassindale, R. (1933).** "1. The relation between the size, age, and time of migration of salmon and sea trout smolts in the River Tees." "2. The proportion of the sexes and the food of smolts of salmon and sea trout in the Tees Estuary." Ministry of Agr. and Fish., Fish. Invest. Ser. 1, 3, No. 4, 1–14. (H.M. Stationery Office, price 9*d.*, postage extra.)

Smolts do not begin their seaward movement until they have reached a certain size (not necessarily the same in all smolts of a given age). This takes place either in the second or third year. "Smolts were found to be indiscriminately carnivorous," the estuarine shrimp *Gammarus duebenii* being the commonest food.

89. Foster, G. (1933). "*Bupalis pinaria* L." Ent. Rec. 45, 27.

Suggests that this moth, first recorded from Ireland in 1890, is not a native there, but has been introduced or re-introduced with the planting of pines from Scotch nurseries. In Ireland this species is now abundant wherever there are well established pine-woods.

90. Fletcher, T. B. (1933). "An Australian Tortricid (*Tortrix postvittana* Walker) in England." Ent. Rec. 45, 165–6.

A well known pest of apple orchards in Australia which might become an established pest in this country also. Three larvae were found in apples imported from New Zealand, but only one of these was reared successfully.

91. Turner, H. J. (1933). "Notes on migratory species of Lepidoptera (mainly Surrey)." Ent. Rec. 45, 127.

Records *Pyrameis cardui*, *P. atalanta*, *Polygonia c-album*, *Macroglossum stellatarum*, *Plusia gamma*, *Pieris brassicae* and *P. rapae*. Further reference in **T. B. Fletcher**, *ibid.* 45, 165.

92. Anon. (1933). "Insect Immigration on the Norfolk Coast." Ent. Mo. Mag. 69, 163–4.

93. Bolam, G. (1933). "Immigrant butterflies about Alston." Vasculum, 19, 121–8.

94. Grimshaw, P. H. (1933). "Butterfly immigration records." Scottish Nat. 156.

Further references by same author, 173–81, and by **L. J. Rintoul** and **E. V. Baxter**, 155–6.

95. Fassnidge, W. (1933). "Immigrant" Lepidoptera." Entomologist, 66, 166–7.

Further references in **N. D. Riley**, *ibid.* 167; **T. Dannreuther**, *ibid.* 167, 186–90, 209–12, 230–4, 251–7 and 268–74; **C. Nicholson**, *ibid.* 285–7; etc.

96. Thompson, G. S. (1933). "Association of Hippoboscids with Lice." Nature, 132, 605.

Gives a number of records of bird-lice (Mallophaga) attached to Hippoboscid flies from birds.

97. Lucas, C. E. (1933). "Occurrence of *Dolioletta gegenbauri* (Uljanin) in the North Sea." Nature, 132, 858.

This pelagic Tunicate normally inhabits warm and tropical waters and indicates abnormal Atlantic inflow into the North Sea. Evidence of diurnal migration is given.

98. Dakin, W. J. (1933). "Unusual occurrence of pelagic organisms." Nature, 131, 239–40.

Great invasion of *Physalia*, *Velella*, and *Ianthina*, in New South Wales, at same time of similar invasion by *Velella* and *Ianthina* in British waters. Additional letter by **G. P. Farran** (p. 240) on tropical animals found south-west of Ireland: he queries the deduction that these invasions indicate influx of Atlantic water and suggests that they originate from abnormal multiplication in warmer regions.

99. Pearsall, W. H. (1933). "*Uroglenopsis americana* in Windermere." Naturalist, 122.

This colonial alga, not previously recorded from Britain, occurred probably for the first time in 1932 in Windermere. The plankton of this lake has shown progressive changes in recent years apparently due to increased organic matter in the water.

Note. The *Journal of the Entomological Society of the South of England* (to be known in future as the "Society for British Entomology"), Vol. 1, part 4, contains notes on the feeding habits of a Mycetophilid larva, immigrant Lepidoptera, second broods of normally single brooded Lepidoptera resulting from the abnormally hot dry summer of 1933, *Pieris rapae* ovipositing and feeding on Primulaceae and Compositae, Lepidopterous hosts of *Phryxe nemea* and *Lydella stabulans* (Dipt., Tachinidae), Dipterous and Hymenopterous parasites bred from Lepidoptera, *Chrysops relictus* (Dipt., Tabanidae) in abundance on South Haven Peninsula, Thomisid spiders and prey, *Aphidius ervi* (Hym., Braconidae) bred from *Macrosiphum amygdaloides* (Hem., Aphididae), Dipteron and Coleopteron visiting Orchids, prey of dragonflies, prey of *Scatophaga stercoraria* (Dipt.) prey of *Cantharis pellucida* (Col.), prey of *Asilus crabroniformis* (Dipt.).